Vocal Communication in Banded Mongoose

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Summary

Animals living in social groups need to coordinate behaviours and decisions, while dealing with group-members in different types of relationships. In many species, communication through vocal signals is essential for this coordination. Hence it has been hypothesised that social complexity is a driving force in the evolution of vocal repertoire sizes, with social animals having larger repertoires than solitary species. A constraining factor in this predicted increase of vocal repertoire sizes is that animals are anatomically restricted in the number of different discrete call types they can produce. Through various mechanisms of flexibility in vocal production, such as the use of calls in sequences or vocal cues, animals could potentially overcome this constraint and increase the potential information content available for the recipient.

In this thesis, I investigated the vocal repertoire of a wild but habituated population of cooperatively breeding banded mongooses (*Mungos mungo*) in their natural habitat. I found that banded mongooses use 15 acoustically discrete call types that show a high degree of variability both within and between call types. I showed that the banded mongoose close calls contain two acoustically different segments: the first being stable and individually distinct, and the second being graded and correlating with the current behaviour of the individual, whether it is digging, searching or moving. Segregation and segmental concatenation of vocal signatures or cues is likely a common, but so far neglected dimension of information coding in animal vocal communication. Further research showed that banded mongooses use these close calls in combination with other call elements potentially resulting in new call types, namely the 'excitement', 'lead', and 'lost' call. The individual distinct segment of the close call remained unchanged in these sequences. The additional elements related to the specific behavioural context not only differed in their acoustic structure, but also in the variation in the number of these elements emitted after the preceding close call. These results show that banded mongooses not only increase their vocal repertoire by varying the acoustic structure of vocalizations as was observed in the close calls and recruitment calls, but also by non-random concatenation of calls into more complex sequences. Together these studies show that through call combinations and vocal cues banded mongooses increase the potential information available to the receivers, despite the graded nature of many of the vocalisations. This ability to convey additional information in their vocalisations might compensate for the reduced number of calls compared to other group living mongoose species.

The studies in this thesis also show that the vocal complexity hypothesis should not only be related to the number of discrete call types, but also to the amount of information potentially conveyed in the vocal repertoire. Affiliative contexts have been hypothesized to be the most relevant when investigating factors related to the social complexity. The results presented in this thesis add to the recent findings that additional dimensions of vocal expressions may be prevalent in affiliative contexts. I therefore argued that whilst investigating the relationship between social complexity and communicative complexity, a focus should be placed on affiliative contexts and all dimensions of acoustic variability that potentially convey information to receivers need to be considered.

Zusammenfassung

In sozialen Gruppen lebende Tiere müssen ihre Verhaltensweisen sowie Entscheidungen koordinieren und dabei die unterschiedlichen Beziehungen zu Gruppenmitgliedern berücksichtigen. In vielen Arten spielt dabei die Kommunikation mithilfe vokaler Signale eine grosse Rolle. Folglich wurde die Hypothese aufgestellt, dass soziale Komplexität eine treibende Kraft in der Evolution der Grösse von Rufrepertoiren ist, wonach soziale Tiere ein grösseres Repertoire haben als einzelgängerische Arten. Als ein restriktiver Faktor wirken dabei anatomische Einschränkungen bezüglich der Anzahl verschiedener diskreter Ruftypen, die produziert werden können. Flexibilität bei der vokalen Produktion durch die Kombination von verschiedenen Ruftypen und vokalen Hinweisen kann dies teilweise ausgleichen und damit den potentiellen Informationsgehalt für den Empfänger erhöhen.

In der vorliegenden Arbeit untersuchte ich das vokale Repertoire einer wilden, habituierten Population von Zebramangusten (*Mungos mungo*) in ihrem natürlichen Habitat, welche ihre Jungen kooperativ aufziehen. An Zebramangusten in ihrem natürlichen Lebensraum, konnte ich zeigen, dass sie über 15 akustisch unterschiedliche Ruftypen verfügen, welche ein hohes Mass an Variabilität sowohl innerhalb als auch zwischen den Ruftypen aufweisen. Weiterhin konnte ich zeigen, dass die Kontaktrufe von Zebramangusten zwei akustisch unterschiedliche Segmente beinhalten: das erste ist stabil und individuell unterschiedlich, während das zweite gradiert vorkommt und mit dem aktuellen Verhalten des Tieres korreliert, wie beispielsweise mit dem Graben und Suchen nach Nahrung oder der gezielten Fortbewegung. Dies stellt einen Hinweis dar für Marlers Hypothese der temporalen Segregation von Information innerhalb eines einsilbigen Ruftyps. Segregation und segmentelle Konkatenation von vokalen Signaturen oder Hinweisen ist wahrscheinlich eine häufige, aber bisher oft vernachlässigte Dimension in der vokalen Tierkommunikation. Ausserdem zeigte sich, dass Zebramangusten diese Kontaktrufe in Kombination mit anderen Rufelementen verwenden, was möglicherweise in neuen Ruftypen resultiert: den sogenannten 'Aufregungs-', 'Leit-' und 'Verlust-' Rufen ('excitement', 'lead', 'lost' calls). Das individuell spezifische Segment des Kontaktrufs bleibt bei diesen Sequenzen unverändert. Die zusätzlichen Elemente bezüglich des spezifischen Verhaltens unterscheiden sich nicht nur in der akustischen Struktur, sondern auch in der Variation der Anzahl dieser Elemente, welche dem Kontaktruf folgen. Diese Ergebnisse zeigen, dass Zebramangusten ihr vokales Repertoire nicht nur durch Variation der akustischen Struktur vergrössern können, wie beispielsweise bei Kontaktrufen und Rekrutierungsrufen. Vielmehr können sie dies auch durch nicht-zufällige Konkatenation von Rufen zu komplexeren Sequenzen. Zusammengenommen demonstrieren diese Studien, dass Zebramangusten mithilfe von Rufkombinationen und vokalen

Hinweisen die potentielle Information für den Empfänger vergrössern können, ungeachtet der Gradierung vieler Rufe. Diese Fähigkeit, durch Kombinationen von akustisch unterschiedlichen Rufsegmenten oder Rufen zusätzliche Information für Empfänger zu generieren, kompensiert möglicherweise die im Vergleich zu anderen gruppenlebenden Mangustenarten reduzierte Rufanzahl.

Die in dieser Arbeit enthaltenen Studien deuten weiter daraufhin, dass die Hypothese bezüglich der Evolution der vokalen Komplexität nicht nur auf die Anzahl diskreter Rufe typen bezogen werden sollte, sondern auch die Variabilität der Kombination von vokalen Einheiten berücksichtigt werden muss. Es wird vermutet, dass affiliative Kontexte bei der Untersuchung von Faktoren bezüglich der sozialen Komplexität eine hohe Relevanz besitzen. Die präsentierten Resultate schliessen sich neuesten Forschungsergebnissen an, dass zusätzliche Dimensionen der vokalen Expression in affiliativen Kontexten verbreitet sind. Bei der Untersuchung der Beziehung zwischen sozialer Komplexität und kommunikativer Komplexität sollte daher ein Fokus auf affiliative Kontexte gelegt werden. Ausserdem sollten alle Dimensionen der vokalen Variation berücksichtigt werden.

General introduction

General introduction

Communication through vocal signals has been shown to be essential in the coordination of many behaviours in animals, such as mate attraction, parent-offspring negotiation, warning group members against danger, sharing information on food locations, vigilance, territorial defence, or maintaining group cohesion (Hauser 1996; Bradbury and Vehrencamp 1998; Seyfarth et al. 2010). Significant differences in the acoustic structure and the usage can be observed between call types. This can be due to call types differing between behavioural contexts or elicited by external events (i.e. context specificity, Owren and Rendall 1997; Bradbury and Vehrencamp 1998; Owren and Rendall 2001; Seyfarth and Cheney 2004; Seyfarth et al. 2010). It might also be due to meaningful variations within a specific call type (i.e. graded variation in acoustic structure of call depending on context, Rendall et al. 1999; Rendall 2003; Yin and McCowan 2004; Furrer and Manser 2009b). Additionally, animals show flexibility in production or usage of vocalisations by call combinations of discrete call types (Crockford and Boesch 2005; Arnold and Zuberbühler 2006a).

A better understanding of an animal's vocalisations and its complete repertoire would enable us to gain further insight into its ecology and social structure. It has also been argued that a comprehension of the selective pressures that determine a species' vocal repertoire is essential in the study of the evolution of animal vocal behaviour (Blumstein and Armitage 1997; Range and Fischer 2004; McComb and Semple 2005). The vocal repertoire of animals is predominately constrained by morphological (Fitch 2000), motivational (Morton 1977; Briefer 2012) and external factors (e.g. habitat constraints, Morton 1975; Ey and Fischer 2009; Ey et al. 2009). Besides these, a species' social environment ('social complexity') has also been hypothesised to affect its vocal repertoire size (Marler 1977; Hauser 1996; Blumstein and Armitage 1997; McComb and Semple 2005; Freeberg et al. 2012).

The characteristics of vocal repertoires

Vocal repertoires generally describe the number of discrete call types an animal produces. In songs of birds and cetacean species a repertoire is often described as the number of songs produced, and not as the number of different single units. Overall vocal repertoires can be distinguished on the basis of inter-specific differences in the structural features of animal vocalisations (Marler 1976; Hauser 1996). Traditionally, repertoires have either been described as 'graded' or 'discrete', or a mixture of the two (Marler 1967; Hauser 1996).

Discrete signals are distinguished from each other by categorical (i.e. stepwise) differences. As there is no gradual transition from one signal to the next, discrete signals are therefore less ambiguous than many graded signals. The digital displays of watches, traffic lights and price tags are good examples of daily-life non-animal discrete signals; there is for instance no gradual shifting from green to yellow to red on traffic lights (OGrady and Archibald 2011). It is thought that discrete signals allow a listener to discriminate easily between one signal type and another (Marler 1976; OGrady and Archibald 2011). Marler (1976) hypothesised that long-distance calls should be acoustically distinct because other cues may be lacking. Additionally, he argued that discrete vocal repertoires should be favoured when auditory signals are used without accompanying visual or other contextual cues, for instance in species living in dense forest habitats.

Gradation is common in many forms of communication. Daily-life non-animal examples of graded signals are the (apparently) graded movement of most clock hands or the needle of a car's speedometer (OGrady and Archibald 2011). Voice volume can also be seen as gradation; the more someone wants to be heard, the louder she/he will speak. As this is a continuous scale, there are no clear steps that can be associated with a specific change in meaning (OGrady and Archibald 2011). A graded vocal system is characterized by continuous acoustic variation between and/or within signal types lacking clear acoustic boundaries between one signal type and the next (Hauser 1996; Range and Fischer 2004).

Many animal signals are graded, such as the barking of dogs (*Canis lupus familiaris*, Yin and McCowan 2004), contact calls in chacma baboon (*Papio cynocephalus ursinus*, Rendall et al. 1999) or the 'trills' of pygmy marmosets (*Cebuella pygmaea*, Snowdon and Pola 1978). It has been hypothesised that graded vocal repertoires evolved when individuals inhabited relatively open habitats and had high rates of interaction with conspecifics at close range (Marler 1976). One of the first detailed attempts to investigate vocal gradation was a long term field study on Japanese macaques (*Macaca fuscata*). Green (1975) showed that there is a strong and consistent relationship between signal grading and circumstances of production in the 'coo' calls of these macaques. Therefore signallers potentially convey subtle and complex information in their calls about the circumstances they are in. Generally graded vocalisations have the potential to be rich of subtle information, but there is a trade-off with precision (Green 1975; Marler and Mundinger 1975).

The classification of signals into graded or discrete is not easy and many signals will be intermediate. Additionally, whilst elements of species' repertoires and human language are classified as graded systems on the production side (Green

1975; Nelson and Marler 1990; Dooling 1992), they are perceived by receivers as a discrete system (Marler 1976; Fischer et al. 1995; Hauser 1996; Fischer and Hammerschmidt 2001; Slocombe et al. 2009). The ability to categorise graded signals as discrete units has been hypothesised to be critical for the evolution of human language (Marler 1975; Marler and Mundinger 1975). Understanding how animals use and perceive graded signals might therefore not only give insights in the potential information available to receivers, but also shed light on the evolution of language related skills (Hauser 1996; Meise et al. 2011).

Flexibility in vocal production

Most animals are anatomically constrained in the number of discrete call types they can produce (Fitch 2000), and animal calls are likely developed under strong genetic constraints (Hammerschmidt and Fischer 2008). Due to significant differences in the vocal production system, cetacean species seem to be an exception in mammals (Hammerschmidt and Fischer 2008). The conventional technique of estimating vocal repertoire sizes is to count the number of discrete sounds (Blumstein and Armitage 1997; McComb and Semple 2005; Gustison et al. 2012). Due to the anatomical constraints vocal repertoire sizes are limited as well. However, there is a growing body of evidence that animals can partially overcome these constraints by showing various forms of vocal flexibility. This flexibility is achieved through a certain degree of variability in both production and usage of existing call types.

One way that would enable animal vocal flexibility is the concatenation of sounds (i.e. calls or syllables) into more complex vocal sequences (Jackendoff 1999; Hauser 2000; Zuberbühler 2002). By combining different vocalisations, signallers have the potential to vastly increase the vocal variation that may convey information available to receivers (Crockford and Boesch 2005; Arnold and Zuberbühler 2006a; Arnold and Zuberbühler 2008). The best known example of combinatorial vocal communication comes from of the putty-nosed monkeys (*Cercopithecus nictitans*), which produce two predator specific alarm calls referring to aerial or terrestrial predators. Receivers respond in an appropriate way upon hearing these vocalisations, suggesting that the calls are meaningful (Arnold and Zuberbühler 2006b). In a different behavioural context these two meaningful alarm calls are combined in a specific order and this combination causes a qualitatively different behavioural response, namely increased group movement (Arnold and Zuberbühler 2006a; Arnold and Zuberbühler 2008). In accordance with this, Campbell's monkeys (*Cercopithecus campbelli*) also have two predator specific alarm call types (Ouattara et al. 2009a). These call types are produced singularly in response to either eagles or leopards, but are also combined with an, in itself meaningless, acoustic element. This meaningless element is added

to the end of the call and it changes the 'meaning' of the alarm call and its associated behavioural response (Ouattara et al. 2009b; Ouattara et al. 2009c). The majority of the studies describe call combinations in the context of alarm calls (Crockford and Boesch 2005; Arnold and Zuberbühler 2006a; Clarke et al. 2006; Arnold and Zuberbühler 2008; Endress et al. 2009; Ouattara et al. 2009b; Ouattara et al. 2009c; Schel et al. 2009; Candiotti et al. 2012), and only a few call combinations have been observed in a wider range of behaviours (e.g. bonobo, *Pan paniscus*, Clay and Zuberbühler 2011; chimpanzee, *P. troglodytes*, Crockford and Boesch 2005 and Diana monkey, *Cercopithecus diana*, Candiotti et al. 2012).

A special type of vocal combinations is formed by the combination of syllables. Syllables (often also referred to as elements) are defined as an uninterrupted trace in a spectrographic signal and they are seen as the basic unit of many bird and some mammalian songs. In contrast to the previously discussed call combination studies, syllables in songs are generally not used singularly and have little to no meaning by themselves (Marler and Slabbekoorn 2004; Berwick et al. 2011). Single syllables generally are combined into sequences, which express 'simple' territorial or courtship display (Marler and Slabbekoorn 2004; Berwick et al. 2011). However, there are examples where apparently meaningless syllables are combined in such a way that they convey multiple levels of information for receivers. For example, white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) express individual identity and group membership in the distinct note complex and trill phrases of their song respectively (Nelson and Poesel 2007). The combination of syllables into these more complex phrases or songs has been well studied and shown in many bird, primate and cetacean species. The combination of these elements is not random and seems to follow strict rules (Payne and McVay 1971; Ford 1989; Fitch and Hauser 2004; Fitch 2010). Such concatenation of separate syllables enables animals to enrich and extend the signalling space as can be seen in songs of birds (Elfstörm 1990; Marler and Slabbekoorn 2004; Nelson and Poesel 2007), rock hyrax (*Procavia capensis*, Koren and Geffen 2009), cetacean (Payne and McVay 1971; Ford 1989), and primate species (Fitch and Hauser 2004; Clarke et al. 2006; Schel et al. 2009).

Animals may also convey additional information in their vocalisations through vocal cues. Cues have not evolved for their effect on receivers (Maynard-Smith and Harper 2003), and may merely be a side-effect of morphological or physiological differences between signallers. However, if the variation reliably correlates with features of signallers, receivers can use them as information and there will be a selective benefit to pay attention to these cues (Hauser 1996; Maynard-Smith and Harper 2003). As cues are the by-products of morphological, motivational or behavioural characteristics of the signaller, they, in contrast to signals, cannot be

switched 'on' and 'off' (Hauser 1996). When related to individual, kin or group identities these cues are often referred to as signatures. For clarity both signatures and cues will be referred to as cues hereafter.

Variation in a call's acoustic structure correlated to signaller's characteristics, such as identity, sex or age, does not mean that this variation is adaptive or that these cues are used by receivers. However, in the last 20 years, studies have shown that many species attend to these, often subtle, acoustic differences and provide useful information to receivers. This is the case for individual discrimination between adults based on identity cues (e.g. emperor penguins, *Aptenodytes forsteri*, Robisson et al. 1993; domestic horses, *Equus caballus*, Proops et al. 2009; and meerkats, *Suricata suricatta*, Townsend et al. 2012), offspring recognition (e.g. northern fur seal, *Callorhinus ursinus*, Insley 2000; Barbary Macaque, *Macaca sylvanus*, Fischer 2004; and Australian sea lion, *Neophoca cinerea*, Charrier et al. 2009), as well as group identities (e.g. greater spear-nosed bat, *Phyllostomus hastatus*, Boughman and Wilkinson 1998; chimpanzee, Crockford et al. 2004 and meerkats, Townsend et al. 2010). Besides these common cues related to identities, acoustic cues were shown to be present in vocalisations that correlated with body size (rhesus macaque, *Macaca mulatta*, Fitch 1997; red deer, *Cervus elaphus*, Reby et al. 1998; Reby and McComb 2003; and fallow deer, *Dama dama*, Vannoni and McElligott 2008), male quality (red deer, Clutton-Brock and Albon 1979; Reby and McComb 2003, baboons, *Papio spp.*, Fischer et al. 2004: and fallow deer, Briefer et al. 2010), sex and reproductive states (giant panda, *Ailuropoda melanoleuca*, Charlton et al. 2009; Charlton et al. 2010).

Animal calls commonly contain combinations of multiple different vocal cue types (Hauser 1996; Bradbury and Vehrencamp 1998; Maynard-Smith and Harper 2003). A variety of acoustic parameters can be related to these different cues. However, as many acoustic parameters are correlated with one another and acoustic space is limited, the amount of variation that can be used by signalers to express different signature types is ultimately constrained (Marler 1960; Briefer et al. 2010). A reduced reliability of at least one of the vocal cues can be the result of this constraint, as it causes a trade-off between the various cues (Marler 1960; Briefer et al. 2010). Marler (1960) observed the conflict between the need for variability between group members to achieve individuality with the need for stereotypic vocalisations for group recognition in bird songs. A similar trade-off has been described between the vocal cues for identity (stable over time) and male quality (variable over time) in fallow deer (Briefer et al. 2010).

Through segregation in either temporally distinct call segments or different acoustic features, this potential trade-off on the accuracy of information available to the receivers could partially be resolved (Marler 1960; Briefer et al. 2010). Although, not always explicitly stated as examples of segregation of information, examples for both mechanisms (i.e. temporal and spatial) have been described. In chacma baboons grunts, the caller's identity is conveyed primarily in the formant structure, whereas context-specific information is conveyed in other acoustic parameters (Owren and Rendall 1997; Rendall et al. 1999). Formants have also been shown to be important for individual distinctiveness in for instance rhesus macaques (Rendall et al. 1998) and giant panda (Charlton et al. 2009). Besides the white-crowned sparrows example, the temporal situation is illustrated by the rock hyraxes, who convey individual identity, body weight, size, condition, social status and hormonal state in various temporally separated components of their complex song (Koren and Geffen 2009). Similar segregation of acoustic properties has been shown in the songs of humpback whales (*Megaptera novaeangliae*, Payne and McVay 1971), killer whales (*Orcinus orca*, Ford 1989) and meadow pipits (*Anthus pratensis*, Elfstörm 1990).

Aim of research

To clarify the importance of the factors such as ecological and social constraints on the observed variation in species' vocal repertoires and the use of vocalisations, it is essential to study animals where detailed and long-term observations are available. Additionally, it is important to study the use of vocalisations under natural conditions in the natural habitat of a species. I conducted my fieldwork for this thesis on a habituated population of wild, but individually recognisable, banded mongooses (*Mungos mungo*). I used detailed behavioural observations, acoustic analysis and playback experiments to investigate the function of various vocalisations in banded mongooses. I focused on the vocal repertoire in general, but also investigated the graded nature of the vocalisations in banded mongooses. My research will provide the scientific community with a better understanding of a graded vocal repertoire of a species with a more egalitarian social systems than that of many other cooperative mongoose species.

Mongooses

Phylogentically, banded mongooses are mammals belonging to the Order Carnivora and the family *Herpestidae*. The family consists of 37 species (Veron et al. 2004; Agnarsson et al. 2010) and they range from mostly solitary species (e.g. the Egyptian mongoose, *Herpestes ichneumon*, and the slender mongoose, *Herpestes sanguineus*), through flexible family living groups (e.g. the yellow mongoose, *Cynictis penicillata*), to the obligatory social breeding banded mongoose and the obligatory cooperatively breeding meerkat and dwarf mongooses (*Helogale parvula,* LeRoux et al. 2009). It has been argued that the main factor for the evolution of sociality in mongooses is communal anti-predator defence (Rood 1986), while in larger carnivores the primary benefit of sociality is the communal hunting of prey (MacDonald 1983). There have been detailed studies on the anti-predator behaviour, communication and social interactions in social mongooses, such as the dwarf mongoose (Rasa 1987; Beynon and Rasa 1989; Rood 1990), meerkat (Clutton-Brock et al. 1998; Manser 1998; Clutton-Brock et al. 1999; Manser et al. 2002) and yellow mongoose (Rasa et al. 1992; LeRoux et al. 2009). The vocal repertoire of the banded mongoose was studied in captivity (Messeri et al. 1987) and in a wild habituated population (De Luca 1998; Müller and Manser 2008; Furrer and Manser 2009a; Metherell 2009). Overall, descriptions of vocal repertoires are available for eight mongooses species (Table 1 in: LeRoux et al. 2009), with various degrees of sociality. Mongooses therefore form an ideal group to study the relationship between the nature of sociality and the vocal repertoire (see Manser 1998; Le Roux et al. 2001, for details and references). This setting offers a unique opportunity to assess whether differences in social organisations and habitat can help us to understand differences in vocal repertoire and call structures.

Study species

Banded mongooses live in extended family groups ('packs') of between 6 and 50+ animals. Hereby they have the largest stable groups for any carnivore (MacDonald and Norris 2001). Most packs consist of a core of breeding adults, a group of younger adults that mainly help and only occasionally breed and a variable number of juveniles and pups from recent breeding attempts (Cant and Field 2001). In contrast to the other social mongooses, breeding in banded mongooses is not restricted to a dominant pair, but multiple males and females are involved in breeding (Cant 2000; De Luca and Ginsberg 2001; Cant et al. 2010; Hodge et al. 2011). Although, there is no apparent relationship between dominance rank and the number of matings in males (De Luca and Ginsberg 2001), paternity is monopolised

by the top three males (Nichols et al. 2010). Eviction has a strong effect on female reproductive success (Cant et al. 2010), but reproductive success is also highly correlated with the female age and condition (De Luca and Ginsberg 2001). Births are highly synchronous, with 64 per cent of females giving birth in the same night. This reduces risk of infanticide of offspring and decreases competition between littermates (Hodge et al. 2011).

After birth, pups remain at the natal den for a period of three to four weeks. During this period at least one adult remains behind to guard them, while the rest of the pack is out foraging (Rood 1974; Rood 1975; Cant and Field 2001). This so-called 'babysitting' is done by all social mongooses (Rood 1986) and has been shown to be costly in meerkats (Clutton-Brock et al. 1998). Following this babysitting period, pups will go out with the pack on foraging trips. Uniquely for mammals, banded mongoose pups form a long-lasting and exclusive association with a specific (non-parental) adult, the so-called 'escort'. Associations are formed in the first few days after emerging and generally remain stable over the next 6 to 8 weeks, the period of dependence (Gilchrist 2004; Hodge 2005). Pups receive the majority of care from their escorts. Escorted pups receive more food, grow faster, have higher survival chance, and reach the age of sexual maturity earlier than non-escorted pups (Hodge 2005). Pups and their escorts do mutually recognise each other's vocalisations (i.e. respectively escort close calls and pup distress calls, Müller and Manser 2008). In the majority of cases pups follow escorts (Gilchrist 2004), but escorts may be vocally stimulating pups to follow them by using increased call rates (pers. obs. David Jansen). These findings suggest that both pups and escorts contribute to the maintenance of the associations (Müller and Manser 2008).

Banded mongooses are diurnal and days are spent foraging away from the natal den. When no pups are at the den, groups normally do not return to the den during the day. Packs forage as a cohesive unit relatively close together, usually with the entire pack within 30 m of one another (Bell 2006). When foraging, group members are often more spread out but group cohesion is presumably maintained by vocalisations, mainly close calls (Rood 1975; Messeri et al. 1987; Müller and Manser 2008). During foraging in or around thickets, banded mongooses scramble through the leaf litter in search of millipedes, little beetles and other invertebrate prey. They regularly dig for food items in the soil with their head down. In the open grass area mongooses fan out in search of ungulate dung piles. These piles are then meticulously taken apart in search of dung beetles and their larvae. Especially at dung of elephant this can lead to high congregation of mongooses, leading to high levels of foraging competition (Rood 1975). Besides insects, small vertebrates, eggs or fruit are opportunistically taken. Nights are spent in a variety of,

mainly below-ground, dens, such as termite mounts, erosion gullies, old burrows of aardvark or warthog, thick vegetation or man made structures. Average stay at den is 2-3 days (Cant 1998), but this is longer in periods of babysitting. Popular dens are regularly reused (Cant 2000). Mongooses do not dig their own dens, but especially in periods of babysitting, some maintenance can be observed.

As banded mongooses are small, mobile, spend considerable time in thick vegetation, and are often visually constrained during foraging, vocalisations are likely to play a critical role in keeping individuals regularly informed of changes in their social and ecological environment (Rood 1975; Messeri et al. 1987; Furrer and Manser 2009a). In contrast to the closely related group living meerkats and dwarf mongoose, banded mongooses have a more graded call repertoire (Messeri 1983; Messeri et al. 1987). Although Messeri et al. (1987) described the nine calls of banded mongoose in captivity, to date, no detailed study exists of the vocal repertoire of the banded mongoose in their natural habitat (but see Metherell 2009, for detailed analysis of pup vocalisations). The graded nature of the vocal repertoire was confirmed in a study of their recruitment calls. The acoustic structure of the recruitment calls graded from more tonal variants in low urgency encounters of secondary predator cues, to calls with a harsher, noisier acoustic structure produced during high urgency encounters with snakes or rival neighbouring packs. This suggests a graded rather than a discrete recruitment call system (Furrer and Manser 2009b).

Study site and population

The data presented in this thesis were collected in three field seasons between February 2009 and July 2011 on a wild, but habituated, population of banded mongooses at the Banded Mongoose Research Project on and around the Mweya peninsula in Queen Elizabeth National Park, Uganda (0°12S; 29°54E). The banded mongooses at this location were first studied in the 1970's by Rood (Rood 1974; Rood 1975; Rood 1983). In 1994 the research was continued by a succession of PhD students and post-doc researchers (Cant 1998; De Luca 1998; Gilchrist 2001; Hodge 2003; Bell 2006; Müller 2007; Furrer 2009; Metherell 2009; Jordan et al. 2010). During the study period the population consisted of about six habituated groups on which detailed observations and experiments could be carried out. The number of groups fluctuated from year to year due to predation, eviction of well-habituated animals, immigration of wild individuals and emigration outside the study area. Group sizes varied from 6 to 50+ individuals and at any point the habituated population consisted of approximately 150 individuals. In contrast to other areas such as the

Serengeti (3 individuals/km^2, Waser et al. 1995), the study population experiences high densities (18 individuals/km^2, Cant 1998; Gilchrist and Otali 2002).

In addition to the habituated groups several semi-habituated groups were followed for long-term life history data. Every group is routinely visited (min. every two or three days) for life history data collection. Groups are located by radio tracking radio-collars (SirTrack Ltd, Havelock North, New Zealand) fitted around the neck of at least one group member. A similar technique used on the meerkats did not entail any cost for the collared individual (Golabek et al. 2008). The territory of one of the groups included large parts of Mweya village, including a safari lodge. The group regularly visited this lodge and gained access to refuge. Two additional groups had regularly access to refuge feeding (Gilchrist and Otali 2002).

The Mweya peninsula lies at the northern shore of the Kazinga Channel at its confluence with Lake Edward. It is connected to the mainland by a narrow isthmus. The peninsula consists of two levels with a steep slope curving from the north-east to the south-west. The lower peninsula (from lake level to approximately 15m above lake level) and the slopes are covered by dense thickets of *Euphorbia candelabrum*, *Azima tetracantha* and *Capparis tomentosa*. These dense '*Euphorbia* forests' are interspersed with more grassy (predominantly *Sporobolus pyramidalis* and *Chloris gayana*) areas. The upper peninsula is more open and grassy, although in recent years bush encroachment by *Capparis tomentosa* and *Acacia spp.* is taking place. The eastern part of the upper peninsula is covered by Mweya village and comprised of the Mweya Safari Lodge, a hostel, staff housing and the buildings of the former Uganda Wildlife Authorities headquarters and the Uganda Institute of Ecology. Annual precipitation is 800-1000 mm (Rood 1975; Gilchrist 2001) and the temperature fluctuates little throughout the year, with a mean daily temperature of 23-26 ° Celsius (Cant 1998). Rain may fall in any month, but the main rainy seasons are March to May and September to November. January to February and June to July are generally the driest months (Rood 1975; Gilchrist 2001).

The peninsula is home to a variety of common herbivores including hippopotamus (*Hippopotamus amphibius*), Ugandan kob (*Kobus kob thomasi*), warthog (*Phacochoerus africanus*), Cape buffalo (*Syncerus caffer*), waterbuck (*Kobus ellipsiprymnus*), giant forest hog (*Hylochoerus meinertzhageni*) and bushbuck (*Tragelaphus sylvaticus*) . Large herds of elephants (*Loxodonta africana*) are regular visitors to the peninsula, but are not permanent residents within the study site. Potential mammalian predators of adult or juvenile banded mongooses include Egyptian mongooses, white-tailed mongooses (*Ichneumia albicauda*), the rusty-spotted genets (*Genetta maculata*), hyenas (*Crocuta crocuta*), lions (*Panthera leo*) and leopards (*Panthera pardus*). In contrast to

previous years, leopards were frequently encountered and were observed to predate on banded mongooses (confirmed sighting by Francis Mwanguhya and Robert Businge). Predatory reptiles include African rock pythons (*Python sebae*; pers. obs.), spitting cobras (*Naja spp.*), African puff adders (*Bitis arietans*) and Nile crocodiles (*Crocodylus niloticus*). Additionally, pups are frequently predated by monitor lizard (*Varanus niloticus*). Among the wide variety of birds of prey, banded mongooses are preyed upon by: African marsh harriers (*Circus ranivorus*), martial eagles (*Polemaetus bellicosus*), yellow-billed kites (*Milvus aegyptius*) and African fish Eagles (*Haliaeetus vocifer*). Additionally, pups are frequently predated by marabou storks (*Leptoptilos crumeniferus*) and, when pups are present, adults regularly alarm at marabou storks.

Outline of thesis

Increased sociality and group living goes along with elevated levels of complexity of relationships between group members and the need to coordinate behaviours to maintain group cohesion. Therefore one would predict it coincides with an increased need for information and therefore communication (Dunbar 1993; Snowdon 2001). Consequently it has been argued that social complexity can drive the evolution of vocal repertoire size (Blumstein and Armitage 1997; McComb and Semple 2005; Burkart and Schaik 2010; Freeberg et al. 2012). Recent studies have shown that animals use a range of different mechanisms to deal with the anatomical constraints that they face in the number of discrete call types they can produce. The chapters in this thesis deal with a range of different dimensions of mechanisms that increase the acoustic variation that may convey information available to receivers. Using detailed behavioural observation, acoustic analysis and playback experiments, I investigate how the social and group-living banded mongooses use vocal signals in their daily lives and how they deal with the graded nature of the vocal repertoire.

In **Chapter 1** I describe the vocal repertoire of the banded mongoose. I discuss the different call types in relation to the contexts they are produced in. Additionally, I discuss whether the predictions of the Morton motivational structure rules fit with some of the observed variations between and within call types. In **Chapter 2** I investigate the vocal signatures in the most frequently used vocalisation, the close call of banded mongooses. I examine how multiple signatures are conveyed in this short single syllable vocalisations. I also propose segmental segmentation to be regarded as an extra dimension in the complexity of conveying information by increasing the acoustic variation of animal vocalisations. The use of call sequences and the implications for the analysis of vocal repertoires is discussed in **Chapter 3**. A range of recent studies has described how various animals use existing calls

into meaningful sequences in the context of danger. Much less emphasis has been on such combinations in more social or affiliative contexts. I describe how banded mongoose use the close calls in call sequences in different affiliative contexts. In **Chapter 4** I present the results of a playback experiment of individual discrimination. Using a violation-of-expectation paradigm I tested if adult banded mongooses use the close calls for individual discrimination. Finally, in the **General discussion** I discuss my results and their implications. I place my findings into the perspective of other findings related to the various dimensions of vocal communication. I then discuss how these recent findings should affect our views on repertoire sizes and comparative studies between species.

This study will add to the knowledge of vocal communication in the family of mongooses. I specifically will investigate how banded mongoose deal with their graded repertoire and if they show efficiency for flexibility in vocal production. Many animals show variable degrees of acoustic flexibility when using vocal signals. These mechanisms range from cues that correlated with the characteristics of the sender to complex song that convey multiple messages. These various dimensions of variations in vocalisations increase the potential information available to receivers. Ignoring these dimensions may lead to an underestimation of the communicative capacities of a species. Overall, my study sheds light on the importance of understanding the variation that underlies animal vocalisations.

References

Agnarsson, I, M Kuntner, and LJ May-Collado (2010). "Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora". *Molecular Phylogenetics and Evolution*, 54(3), 726–745.

Arnold, K and K Zuberbühler (2006b). "The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini*". *Animal Behaviour*, 72(3), 643–653.

— (2006a). "Language evolution: Semantic combinations in primate calls". *Nature*, 441(7091), 303.

— (2008). "Meaningful call combinations in a non-human primate". *Current Biology*, 18(5), R202–R203.

Bell, MBV (2006). "Communication, cooperation and conflict in banded mongooses." PhD thesis. Cambridge, UK: University of Cambridge.

Berwick, RC et al. (2011). "Songs to syntax: the linguistics of birdsong". *Trends in Cognitive Sciences*, 15(3), 113–121.

Beynon, P and OAE Rasa (1989). "Do dwarf mongoose have a language - warning vocalizations transmit complex information". *South African journal of Science*, 85(7), 447–450.

Blumstein, DT and KB Armitage (1997). "Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls". *American Naturalist*, 150(2), 179–200.

Boughman, JW and GS Wilkinson (1998). "Greater spear-nosed bats discriminate group mates by vocalizations". *Animal Behaviour*, 55(6), 1717–1732.

Bradbury, JW and SL Vehrencamp (1998). *Principles of animal communication*. New York: Sinauer Associates.

Briefer, EF (2012). "Vocal expression of emotions in mammals: mechanisms of production and evidence". *Journal of Zoology*, 288(1), 1–20.

Briefer, E, E Vannoni, and AG McElligott (2010). "Quality prevails over identity in the sexually selected vocalisations of an ageing mammal". *BMC Biology*, 8(35), 1–15.

Burkart, JM and CP van Schaik (2010). "Cognitive consequences of cooperative breeding in primates?" *Animal Cognition*, 13(1), 1–19.

Candiotti, A, K Zuberbühler, and A Lemasson (2012). "Context-related call combinations in female Diana monkeys". *Animal Cognition*, 15(3), 327–339.

Cant, MA (1998). "Communal breeding in banded mongooses and the theory of reproductive skew". PhD thesis. Cambridge, UK: University of Cambridge.

— (2000). "Social control of reproduction in banded mongooses". *Animal Behaviour*, 59(1), 147–158.

Cant, MA and J Field (2001). "Helping effort and future fitness in cooperative animal societies". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268(1479), 1959–1964.

Cant, MA et al. (2010). "Reproductive control via eviction (but not the threat of eviction) in banded mongooses". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 277(1691), 2219–2226.

Charlton, BD, Z Zhang, and RJ Snyder (2009). "Vocal cues to identity and relatedness in giant pandas (*Ailuropoda melanoleuca*)". *Journal of the Acoustical Society of America*, 126(5), 2721–2732.

Charlton, BD et al. (2010). "Female giant panda (*Ailuropoda melanoleuca*) chirps advertise the caller's fertile phase". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 277(1684), 1101–1106.

Charrier, I, B Pitcher, and R Harcourt (2009). "Vocal recognition of mothers by Australian sea lion pups: individual signature and environmental constraints." *Animal Behaviour*, 78(5), 1127–1134.

Clarke, E, UH Reichard, and K Zuberbühler (2006). "The syntax and meaning of wild gibbon songs". *PLoS ONE*, 1(1), e73.

Clay, Z and K Zuberbühler (2011). "Bonobos extract meaning from call sequenses". *PLoS ONE*, 6(4), e18786.

Clutton-Brock, TH and SD Albon (1979). "The roaring of red deer and the evolution of honest advertising". *Behaviour*, 69, 145–170.

Clutton-Brock, TH et al. (1998). "Costs of cooperative behaviour in suricates (Suricata suricatta)". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265(1392), 185–190.

Clutton-Brock, TH et al. (1999). "Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*". *Journal of Animal Ecology*, 68(4), 672–683.

Crockford, C and C Boesch (2005). "Call combinations in wild chimpanzees". *Behaviour*, 142, 397–421.

Crockford, C et al. (2004). "Wild chimpanzees produce group-specific calls: a case for vocal learning?" *Ethology*, 110(3), 221–243.

De Luca, DW (1998). "The socio-ecology of a plural breeding species: the banded mongoose, *Mungos mungo*, in Queen Elizabeth National Park, Uganda". PhD thesis. London, UK: University of London.

De Luca, DW and JR Ginsberg (2001). "Dominance, reproduction and survival in banded mongooses: towards an egalitarian social system?" *Animal Behaviour*, 61(1), 17–30.

Dooling, RJ (1992). "Hearing in birds". In: *The Evolutionary Biology of Hearing*. Ed. by DB Webster, RR Fay, and AN Popper. Berlin Heidelberg: Springer, pp. 545–560.

Dunbar, RIM (1993). "Coevolution of neocortical size, group size and language in humans". *Behavioral and Brain Sciences*, 16(4), 681–735.

Elfstörm, ST (1990). "Responses of territorial meadow pipits to strange and familiar song phrases in playback experiments". *Animal Behaviour*, 40(4), 786–788.

Endress, AD et al. (2009). "Evidence of an evolutionary precursor to human language affixation in a non-human primate". *Biology Letters*, 5(6), 749–751.

Ey, E and J Fischer (2009). "The acoustic adaptation hypothesis - a review of the evidence from birds, anurans and mammals". *Bioacoustics*, 19(1-2), 21–48.

Ey, E et al. (2009). "Wild female olive baboons adapt their grunt vocalizations to environmental conditions". *Ethology*, 115(5), 493–503.

Fischer, J (2004). "Emergence of individual recognition in young macaques." *Animal Behaviour*, 67(4), 655–661.

Fischer, J and K Hammerschmidt (2001). "Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls." *Animal Cognition*, 4(1), 29–35.

Fischer, J, K Hammerschmidt, and D Todt (1995). "Factors affecting acoustic variation in Barbary macaque (*Macaca sylvanus*) disturbance calls". *Ethology*, 101(1), 51–66.

Fischer, J et al. (2004). "Baboon loud calls advertise male quality: acoustic features and relation to rank, age, and exhaustion." *Behavioral Ecology and Sociobiology*, 56(2), 140–148.

Fitch, WT (1997). "Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques". *Journal of Acoustical Society of America*, 102, 1213–1222.

— (2000). "Skull dimensions in relation to body size in nonhuman primates: the causal bases for acoustic allometry." *Zoology*, 103(1-2), 40–58.

— (2010). *The evolution of language*. Cambridge, UK: Cambridge University press.

Fitch, WT and MD Hauser (2004). "Computational Constraints on Syntactic Processing in a Nonhuman Primate." *Science*, 303(5656), 377–380.

Ford, JKB (1989). "Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia". *Canadian journal of Zoology*, 67(3), 727–745.

Freeberg, TM, RIM Dunbar, and TJ Ord (2012). "Social complexity as a proximate and ultimate factor in communicative complexity". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1785–1801.

Furrer, RD (2009). "Leadership and group-decision-making in banded mongooses (*Mungos mungo*)". PhD thesis. Zurich, Switzerland: University of Zurich.

Furrer, RD and MB Manser (2009a). "Banded mongoose recruitment calls convey information about risk and not stimulus type". *Animal Behaviour*, 78(1), 195–201.

— (2009b). "The Evolution of Urgency-Based and Functionally Referential Alarm Calls in Ground-Dwelling Species". *American Naturalist*, 173(3), 400–410.

Gilchrist, JS (2001). "Reproduction and pup care in the communal breeding banded mongoose". PhD thesis. Cambridge, UK: University of Cambridge.

Gilchrist, JS (2004). "Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance". *Behavioral Ecology*, 15(6), 952–960.

Gilchrist, JS and E Otali (2002). "The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose". *Canadian journal of Zoology*, 80(10), 1795–1802.

Golabek, KA, NR Jordan, and TH Clutton-Brock (2008). "Radiocollars do not affect the survival or foraging behaviour of wild meerkats". *Journal of Zoology*, 274(3), 248–253.

Green, S (1975). "Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study". *Primate Behavior, Developments in Field and Laboratory Research*, 2, 1–102.

Gustison, ML, A le Roux, and TJ Bergman (2012). "Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1847–1859.

Hammerschmidt, K and J Fischer (2008). "Constraints in primate vocal production". In: *The evolution of communicative creativity: From fixed signals to contextual flexibility*. Ed. by U Griebel and K Oller. Cambridge, MA: The MIT Press, pp. 93–119.

Hauser, MD (1996). *The evolution of communication*. Cambridge, MA: MIT Press.

— (2000). "A primate dictionary? Decoding function and meaning of another species' vocalisations". *Cognitive science*, 24(3), 445–475.

Hodge, SJ (2003). "Evolution of helping behaviour in the communally breeding banded mongoose (*Mungos mungo*)". PhD thesis. Cambridge, UK: University of Cambridge.

— (2005). "Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 272(1580), 2479–2484.

Hodge, SJ, MBV Bell, and MA Cant (2011). "Reproductive competition and the evolution of extreme birth synchrony in a cooperative mammal". *Biology Letters*, 7(1), 54–56.

Insley, S (2000). "Long-term vocal recognition in the northern fur seal." *Nature*, 406(6794), 404–405.

Jackendoff, R (1999). "Possible stages in the evolution of the language capacity". *Trends In Cognitive Sciences*, 3, 272–279.

Jordan, NR et al. (2010). "Scent marking within and between groups of wild banded mongooses". *Journal of Zoology*, 280(1), 72–83.

Koren, L and E Geffen (2009). "Complex call in male rock hyrax: a multi-information distributing channel." *Behavioral Ecology and Sociobiology*, 63(4), 581–590.

Le Roux, A, TP Jackson, and MI Cherry (2001). "The effect of changing call duration and calling bouts on vigilance in Brants' whistling rat, *Parotomys brantsii*". *Behaviour*, 138, 1287–1302.

LeRoux, A, MI Cherry, and MB Manser (2009). "The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality". *Naturwissenschaften*, 96(5), 575–584.

MacDonald, DW (1983). "The ecology of carnivore social behaviour". *Nature*, 301(5899), 379–384.

MacDonald, D and S Norris (2001). *The New Encyclopedia of Mammals*. 1st ed. Vol. 1. New York: Oxford University Press.

Manser, MB (1998). "The evolution of auditory communication in suricates, *Suricata suricatta*". PhD thesis. Cambridge, UK: University of Cambridge.

Manser, MB, RM Seyfarth, and DL Cheney (2002). "Suricate alarm calls signal predator class and urgency". *Trends In Cognitive Sciences*, 6(2), 55–57.

Marler, P (1967). "Animal Communication Signals". *Science*, 157(3790), 769–774.

— (1975). "On the origin of speech from animal sounds." In: *The role of speech in language*. Ed. by J Kavanagh and J Cutting. Cambridge, MA: MIT Press. Chap. On the origin of speech from animal sound, pp. 11–37.

— (1976). "Social organization, communication and graded signals the chimpanzee and the gorilla". In: *Growing points in ethology*. Ed. by PPG Bateson and RA Hinde. Cambridge: Cambridge University Press, pp. 239–281.

Marler, P (1977). "The evolution of communication". In: *How animals communicate*. Ed. by TA Sebeok. Bloomington: Indiana University Press, pp. 45–70.

Marler, P and PC Mundinger (1975). "Vocalizations, social-organization and breeding biology of twite *Acanthus flavirostris*". *Ibis*, 117, 1–6.

Marler, P and H Slabbekoorn (2004). *Nature's Music The Science of Birdsong*. Ed. by P Marler and H Slabbekoorn. San Diego: Elsevier.

Marler, P (1960). "Bird song and mate selection". In: *Animal sounds and communication*. Ed. by W Lanyon and W Tavalga. Port Jervis, NY: Lubrecht & Cramer, pp. 348–367.

Maynard-Smith, J and D Harper (2003). *Animal Signals*. New York: Oxford University Press.

McComb, K and S Semple (2005). "Co-evolution of vocal communication and sociality in primates". *Biology Letters*, 1(4), 381–385.

Meise, K et al. (2011). "Sources of acoustic variation: Implications for production specificity and call categorization in chacma baboon (Papio ursinus) grunts". *Journal of the Acoustical Society of America*, 129(3), 1631–1641.

Messeri, P (1983). "A preliminary comparison between social behaviors of 2 viverrids, the dwarf mongoose and the banded mongoose, in Somalia". *Italian journal of Zoology*, 17(2), 200–200.

Messeri, P et al. (1987). "A study of the vocal repetoire of the banded mongoose (*Mungos mungo*)". *Italian journal of Zoology*, 19(22), 341–73.

Metherell, B (2009). "Offspring care and communication in the banded mongoose". PhD thesis. Cambridge, UK: University of Cambridge.

Morton, ES (1975). "Ecological sources of selection on avian sounds". *American Naturalist*, 109(965), 17–34.

— (1977). "Occurance and significance of motivation structural rules in some bird and mammal sounds". *American Naturalist*, 111(981), 855–869.

Müller, CA (2007). "Environmental knowledge in the banded mongoose *Mungos mungo*". PhD thesis. Zurich, Switzerland: University of Zurich.

Müller, CA and MB Manser (2008). "Mutual recognition of pups and providers in the cooperatively breeding banded mongoose". *Animal Behaviour*, 75(5), 1683–1692.

Nelson, DA and P Marler (1990). "Categorical perception of natural stimulus continuum: birdsong". *Science*, 244(4907), 976–979.

Nelson, DA and A Poesel (2007). "Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song". *Animal Behaviour*, 74(4), 1073–1084.

Nichols, HJ et al. (2010). "Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose". *Animal Behaviour*, 80(4), 649–657.

OGrady, WO and J Archibald (2011). *Contemporary Linguistics: An Introduction*. Ed. by WO O'Grady and J Archibald. 6th. Belford/St. Marin's.

Ouattara, K, A Lemasson, and K Zuberbühler (2009c). "Campbell's Monkeys Use Affixation to Alter Call Meaning". *PLoS ONE*, 4(11), e7808.

— (2009b). "Campbell's monkeys concatenate vocalizations into context-specific call sequences". *Proceedings of the National Academy of Sciences of the United States of America*, 106(51), 22026–22031.

— (2009a). "Anti-predator strategies of free-ranging Campbell's monkeys". *Behaviour*, 146, 1687–1708.

Owren, MJ and D Rendall (1997). "An affect-conditioning model of nonhuman primate vocal signaling". *Perspectives in Ethology*, 12, 299–346.

— (2001). "Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling". *Evolutionary Anthropology*, 10, 58–71.

Payne, RS and S McVay (1971). "Songs of humpback whales". *Science*, 173(3991), 57–64.

Proops, L, K McComb, and D Reby (2009). "Cross-modal individual recognition in domestic horses (*Equus caballus*)". *Proceedings of the National Academy of Sciences of the United States of America*, 106(3), 947–951.

Range, F and J Fischer (2004). "Vocal Repertoire of Sooty Mangabeys (*Cercocebus torquatus atys*) in the Taï National Park". *Ethology*, 110(4), 301–321.

Rasa, OAE (1987). "The dwarf mongoose: a study of behavior and social structure in relation to ecology in a small, social carnivore." *Advances in the Study of Behavior*, 17, 121–163.

Rasa, OAE et al. (1992). "Reproduction in the yellow mongoose revisited". *South Afican journal of Zoology*, 27(4), 192–195.

Reby, D and K McComb (2003). "Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags". *Animal Behaviour*, 65(3), 519–530.

Reby, D et al. (1998). "Individuality in the groans of fallow deer (*Dama dama*) bucks". *Journal of Zoology*, 245(1), 79–84.

Rendall, D (2003). "Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons." *Journal of the Acoustical Society of America*, 113(6), 3390–3402.

Rendall, D, MJ Owren, and PS Rodman (1998). "The role of vocal tract filtering in identity cueing in rhesus monkey (*Macaca mulatta*) vocalizations". *Journal of the Acoustical Society of America*, 103(1), 602–614.

Rendall, D et al. (1999). "The meaning and function of grunt variants in baboons". *Animal Behaviour*, 57(3), 583–592.

Robisson, P, T Aubin, and JC Bremond (1993). "Individuality in the Voice of the Emperor Penguin *Aptenodytes forsteri*: Adaptation to a Noisy Environment". *Ethology*, 94(4), 279–290.

Rood, JP (1974). "Banded Mongoose Males Guard Young". *Nature*, 248(5444), 176–176.

— (1975). "Population dynamics and food habits of the banded mongoose". *East Africa Wildlife journal*, 13, 89–111.

— (1983). "Banded Mongoose Rescues Pack Member from Eagle". *Animal Behaviour*, 31(11), 1261–1262.

— (1986). "Ecology and social evolution in the mongooses". In: *Ecological aspects of social evolution*. Ed. by D Rubenstein and RW Wrangham. Princeton: Princeton University Press, pp. 131–152.

— (1990). "Group size, survival, reproduction, and routes to breeding in dwarf mongooses." *Animal Behaviour*, 39(3), 566–572.

Schel, AM, S Tranquilli, and K Zuberbühler (2009). "The alarm call system of two species of black-and-white colobus monkeys (*Colobus polykomos* and *Colobus guereza*)". *Journal of Comparative Psychology*, 123(2), 136–150.

Seyfarth, RA et al. (2010). "The central importance of information in studies of animal communication". *Animal Behaviour*, 80(1), 3–8.

Seyfarth, RM and DL Cheney (2004). "Meaning and Emotion in Animal Vocalizations". In: *Annals of the NY Academy of Sciences. Emotions Inside Out: 130 Years after Darwins The Expression of the Emotions in Man and Animals*. Ed. by P Ekman et al. Vol. 1000, pp. 32–55.

Slocombe, KE, SW Townsend, and K Zuberbühler (2009). "Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: Evidence from a playback study". *Animal Cognition*, 12(3), 441–449.

Snowdon, CT (2001). "Social processes in communication and cognition in callitrichid monkeys: a review". *Animal Cognition*, 4(3), 447–257.

Snowdon, C and Y Pola (1978). "Interspecific and intraspecific responses to synthezised pygmy marmoset vocalizations". *Animal Behaviour*, 26(1), 192–206.

Townsend, SW, C Allen, and MB Manser (2012). "A simple test of vocal individual recognition in wild meerkats". *Biology Letters*, 8(2), 179–182.

Townsend, SW, LI Hollen, and MB Manser (2010). "Meerkat close calls encode group-specific signatures, but receivers fail to discriminate". *Animal Behaviour*, 80(1), 133–138.

Vannoni, E and AG McElligott (2008). "Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males". *PLoS ONE*, 39, e3113.

Veron, G et al. (2004). "Molecular systematics and origin of sociality in mongooses (*Herpestidae*, Carnivora)". *Molecular Phylogenetics and Evolution*, 30(3), 582–598.

Waser, PM et al. (1995). "Habitat variation and mongoose demography." In: *Serengeti II: dynamics, management, and conservation of an ecosystem*. Ed. by A Sinclair and A P. Chicago: University of Chicago Press., pp. 421–447.

Yin, S and B McCowan (2004). "Barking in domestic dogs: context specificity and individual identification". *Animal Behaviour*, 68(2), 343–355.

Zuberbühler, K (2002). "A syntactic rule in forest monkey communication". *Animal Behaviour*, 63(2), 293–299.

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Vocal repertoire of the banded mongoose

Vocal repertoire of the banded mongoose

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Abstract

Identifying the selective pressures that shape and determine type and sizes of vocal repertoires is a prerequisite for the understanding of a species' specific vocal behaviour and its flexibility. A better knowledge on vocal repertoires of different species will also enable us to increase comparative studies to identify key selective pressures explaining the wide variety of vocal complexity between species. Mongooses (*Herpestidae spp.*) are a good taxonomical group for investigating the influence of sociality on vocal complexity. Here we investigate the vocal repertoire of the communally breeding banded mongoose (*Mungos mungo*). Using a combination of detailed observations and recordings, we present descriptions of the call structure and the function for the range of calls used by this cooperatively breeding mongoose in a range of behavioural contexts. We assessed intra- and inter-call type acoustic variability, using temporal, frequency and waveform parameters. We found that the vocal repertoire of the banded mongoose consists of at least 15 call types. Many of the call types show a high degree of variability within call types in temporal parameters such as duration, and acoustic parameters, such as fundamental frequency, bandwidth and the degree of frequency modulations. Compared to other obligate social species mongooses, the banded mongoose has a more graded vocal repertoire and a reduced number of discrete call types. We argue that these differences may be due to an interplay of social and habitat related factors.

Keywords: vocal repertoire, graded calls, Morton's motivational structure rules , banded mongoose

Background

Revealing the selective pressures that shape the structure of vocalisations, determine type and sizes of vocal repertoires and the overall complexity of vocal expression is one of the prerequisites in the study of the evolution non-human animal species' (hereafter animals) vocal behaviour (Blumstein and Armitage 1997; Range and Fischer 2004; McComb and Semple 2005). Although the vocal repertoire of animals are predominately constrained by morphological (Fitch 2000), motivational (Morton 1977; Briefer 2012) and external factors (e.g. habitat constraints, Morton 1975; Ey and Fischer 2009), a species social environment ('social complexity') has also been predicted to affect its vocal repertoire size ('vocal complexity', Marler 1977; see Freeberg et al. 2012a; Freeberg et al. 2012b for a review).

The 'vocal complexity' hypothesis has been supported by evidence in some primate, rodent and bird species. In other taxa evidence has been tentatively or absent (Freeberg et al. 2012a; Ord and Garcia-Porta 2012). This is partially due to limited data on repertoire sizes in comparable species. The social systems of the 37 species of the mongoose family (*Herpestidae*, Veron et al. 2004; Agnarsson et al. 2010) range from solitary living to obligatory cooperatively breeding. They often live in comparable habitats and are facing similar predation pressures. They therefore form an ideal group to investigate the effects of sociality on vocal complexity (see Le Roux et al. 2008, for references and details).

Another aspect that limits comparative studies is the acoustic difference between vocal repertoires. Animals' vocal repertoires have commonly been classified as being acoustically discrete or graded (Marler 1967; Hammerschmidt and Fischer 1998; Keenan et al. 2013). The separation is made on the basis of interspecific differences in the level of acoustic variation between and within call types (Marler 1976; Hauser 1996).

A graded vocal repertoire is characterized by continuous acoustic variation between and/or within call types lacking distict acoustic boundaries between one call type and the next (Hauser 1996; Range and Fischer 2004). Calls may be graded along acoustic dimensions such as, frequency (commonly known as 'pitch'), severity of frequency modulation, or intensity or duration. Although within this continuum certain intermediate forms may be more prevalent, the lack of distinct boundaries between call types makes their classification difficult (Marler and Mundinger 1975; Hammerschmidt and Fischer 1998; Keenan et al. 2013). Generally graded vocal systems differ from discrete systems in the amount of detail that can be conveyed in the vocalisations. Hence they have the potential to be rich of subtle information, but there is a trade-off with precision (Green 1975; Marler and Mundinger 1975).

In discrete vocal system these intermediate forms are uncommon or absent. Call types are therefore acoustically distinct from another and can 'easily' be discriminated and classified (Marler 1975; Marler 1976; Hauser 1998; Bouchet et al. 2012; Keenan et al. 2013). Variation within call types tends to be limited and therefore the potential to convey additional information is limited. However, as calls lack the ambiguity that is associated with graded calls, they are less likely to be misinterpreted by receivers.

Although the discrete versus graded classification is often presented as a dichotomous system, it is rather a continuum and many species are likely to have a mixed system. The evolution of graded versus discrete signalling vocal systems and the underlying selective pressures are not well understood.

An additional source of variation within call types is the motivational state of the caller. The effect of motivation on animal vocalisations has been widely observed and has been cited in many studies as a reason of additional variation in animal vocalisations (Briefer 2012). For instance, additionally to the discrete functional referential alarm calls of meerkats (*Suricata suricatta*), which do not follow a linear change based on predator type, the calls of meerkats convey information about the level of urgency along a general common rule (Manser 2001; Manser 2010). The Morton's motivational structure rules (hereafter MS rules, Morton 1977) describe the predicted effects of the motivational state of the caller on the acoustic structure of its calls. That is calls produced: *i.*) in aggressive contexts tend to be noisy and have a low fundamental frequency and *ii.*) in fearful/submissive contact are higher pitched and tonal (Morton 1977; Morton 1982; Briefer 2012).

In this paper we investigated the vocal repertoire of the cooperatively breeding banded mongooses. Banded mongoose are a small social carnivore ($\leq$ 2 kg), commonly found in the savannah and open forests of central and eastern Africa. They forage in cohesive units and cooperate in predator avoidance, territory defence and pup care (Rood 1974; Rood 1975; Cant 2003; Gusset 2007). Despite the usually rather egalitarian social system, there is competition between group members and aggressive evictions do occur (De Luca and Ginsberg 2001; Cant et al. 2010; Nichols et al. 2010). They use a range of vocalisations to coordinate these behaviours (Rood 1975; Masi et al. 1987; Messeri et al. 1987). Despite these previous studies there is no comprehensive complete overview of the vocal repertoire and call use of the banded mongoose in the wild. In this chapter a detailed description of the vocal repertoire of the banded mongoose will be presented. We describe the different call types and in relation to the context in which they were given. Furthermore we examine whether the banded mongoose call types fit the predictions of the MS

rules. We conclude by making some comparisons with the vocal repertoires of other mongoose species.

Methods

Study population

Data for adults were collected from February 2009 and July 2011 on a wild but habituated population of banded mongooses living on and around Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12′*S*; 29°54′*E*; for details of the study area see Cant 1998; Gilchrist and Otali 2002. Four (in 2011) to six groups (in 2009 to 2010) of habituated banded mongooses totalling around 150 adult individuals allowed close-range observations (for more details on study population see Cant 1998; Jordan et al. 2010). Animals were classified as adults (≥12 months), sub-adults (6-12 months), juveniles (3-6 months) and pups (≤3 months). For individual identification in the field, adults were marked by shaving a small area of fur of the rump or fitted with colour coded plastic collars, sub-adults and infants were marked by small shavings and pups were individually marked by colouring small areas of fur with blonde hair–dye (Cant 1998; Jordan et al. 2010). As part of the Banded Mongoose Project's long term data collection protocol all animals were additionally tagged with subcutaneous transponders (TAG-P-122GL, Wyre Micro Design Ltd, UK). Trapping and experiments were conducted in accordance with ASAB/ABS guidelines for the use of animals in research.

Recording methods

Vocalisations were recorded from well habituated adult banded mongooses at a distance of approximately 1-2 m, using a Sennheiser directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40-20′000 Hz ± 2.5 dB, Old Lyme, Connecticut, U.S.A.) connected to a Marantz PMD-660 solid state (Marantz Japan Inc.), or a M-Audio Microtrack II (Avid Technology USA Inc). Calls were recorded as part of detailed behavioural focal watches or during *Ad Libitum* sampling recording sessions (Altman 1974). Calls were recorded in wave audio file format (wav) with 16 bits and 44.1 kHz. Whenever possible the identity of the caller was noted and where applicable and possible additional information such as the identity of the social partner, stimulus eliciting the call and distance to threat were also noted. Due to the sporadic use of some of the less common vocalisations and the unpredictability, for instance alarm calls, recordings were affected by circumstantial difficulties. It was therefore not possible to standardise distances between callers and the microphone. Some acoustic parameters such as peak frequency can be

affected by distance between microphone and vocaliser. However, since all vocal recordings were equally affected by this problem, we do not expect a bias effect.

Categorization of arousal variation

To investigate the effects of the caller's arousal level on the acoustic structure of the vocalisations, we used natural observations to assess the behavioural context of call emission. We assigned call types related to specific behavioural context to the MS rules categories based on *i*.) level of fear (N = no fear, S = suspicious, F= fearful) and *ii*.) level of aggressiveness (N = no aggression, M = medium aggression, F = fully aggressive; after Manser 1998). We categorised all different calls according to their acoustical structure. We based the categorisation on the two main predictions of the MS rules; *i*.) the frequency range (low, medium or high); *ii*.) tonality (pure tonal, tonal with noisy parts or mainly noisy).

Acoustic analysis

Calls for analysis were selected based on a good sound-to-noise ratio using Cool Edit 2000 (Syntrillium Software Corp., Phoenix, USA) or Avisoft SASLab Pro 5.18 (R. Specht, Berlin, Germany) (Specht 2012). We did not have sufficient good quality recordings for all call types to be included in the acoustic and statistical analysis. We included 12 call types in the analysis. To generate spectrograms of calls we carried out a 1.024 point fast Fourier transformation (Gauss window, overlap: 93.75%, time resolution 1.45 ms, frequency resolution: 43 Hz). We used a batch processing option to obtain automatic measurements for a range of acoustic parameters of the various parts of the calls. The automatic measurements were checked by visual inspection of the graphic results of the measurements in the spectrograms. Including many acoustic parameters enables an analysis of complex patterns without *a priori* assumptions of the importance of specific parameters (Schrader and Hammerschmidt 1997). Analyses included parameters describing temporal, frequency and waveform related aspects of the various call types. For frequency related parameters we chose the maximum, mean and relative standard deviation (RSD) of the spectrum of the entire element. The RSD is the standard deviation divided by the mean. Higher values of RSD indicate increased parameter variation. The fundamental frequency is defined as the lowest frequency of a periodic waveform and represents the pitch of the sound. Peak frequency is the frequency with the highest amplitude. The peak amplitude is the amplitude of the peak frequency. The duration from the start of the call to the location of the peak amplitude is the distance to max value. The maximum frequency is the lowest frequency of the amplitude exceeding this threshold (-20dB), whilst the maximum

frequency is the highest frequency of the amplitude exceeding the same threshold. The bandwidth is the difference between minimum and maximum frequency where any energy above the threshold is detected. The quartile variables characterize the distribution of energy across the spectrum and indicate the frequency below which 25, 50 or 75% respectively of the energy can be found. The distance between quartile 75% and quartile 25% is a measure of the pureness of the sound. The 50% quartile also indicated the mean frequency. All mean frequency measures were obtained from the mean spectrum of each call or call component, while the 3 quartiles were also measured from the point within the call or call component that had the maximum amplitude. The harmonic-to-noise (HNR) parameter quantifies the ratio of harmonic to non-harmonic energy. Entropy quantifies the randomness (or pureness) of sounds. It is the ratio of the geometric mean to the arithmetic mean of the spectrum. Theoretically it is zero for pure-tone signals and one for random noise. The peak-to-peak amplitude determines the broad-band peak-to-peak amplitude and is related to the peak frequency of the FFT spectrum (Specht 2012). Lastly, for the elements, we used peak frequency values that were measured every 10 ms from the start to the end of the call to get an approximation of the temporal variation in the calls. The number of measured values depended on the duration of the call (n = total duration of the call ()ms) / 10 + 1). We used these values to calculate the maximum (max frequency step) and average (mean frequency step) frequency differences between steps of 10 ms (Charrier et al. 2010).

Statistical analysis

Statistical analyses were performed using R, version 2.15.2 (R Core Team 2012), using the software packages 'HH' (Heiberger 2012) 'klaR' (Weihs et al. 2005), 'lme4' (Bates 2011), and 'MASS' (Venables and Ripley 2002). Discriminant function analysis (DFA) method identifies linear combinations of predictor variables that best characterize the differences among call types and combines the selected acoustic variables into one or more discriminant functions, depending on the number of groups to be classified (Venables and Ripley 2002; Weihs et al. 2005). It provides a classification procedure that assigns each call to its appropriate class (correct assignment) or to another class (incorrect assignment). It has been argued that conventional DFA provides largely inflated levels of overall significance of discriminability when using multiple samples of the same individual (Mundry and Sommer 2007). Therefore the acoustic parameters (hereafter parameters) of only one randomly chosen call per individual per call type were entered into the DFA. We controlled for collinearity between the parameters by using a variation inflation factors analysis (VIF). VIF is a simple diagnostic method to detect evidence of collinearity between parameters.

As only predictory parameters are involved with collinearity, the calculation of VIF is a function of the predictors X's but not of response Y. The VIF for a parameter i is $1/(1-R_i^2)$, where R_i^2 is the R^2 from a regression of predictor i against the remaining predictors. If R_i^2 is close to 1, this means that predictor i is well explained by a linear function of the remaining predictors, and, therefore, the presence of predictor i in the model is redundant. Only parameters with VIF values below 5 were included in the further analysis, as higher values are considered to be evidence of collinearity (Heiberger and Holland 2004; Heiberger 2012). The remaining parameters were entered to a stepwise forward parameter selection. The initial model was defined by starting with the parameter which separates the call types the best. The model was then extended by including further parameters depending on the criteria that the additional parameter i.) minimized the Wilks λ, and ii.) its associated p-value still showed a statistical significance. The selected parameters were subsequently entered to a DFA. For external validation, we used a leave-one-out cross-validation procedure and estimated the significance levels for correct statistical assignment of calls using post hoc 'bootstrapping' analyses. This method determined the probability that a cross-validated correct assignment value was achieved by chance (Müller and Manser 2008a). Using a similar approach we invested the influence of arousal and the fit to the MS rules predictions. Using an additional DFA analysis, we evaluated distinctiveness between the call types that were assigned to the various categories of fear and aggressiveness (Table 5). Using Kruskal-Wallis tests we examined how single acoustical parameters changed with either call type or MS rule categories. We used the Holm–Bonferroni method to adjust the p-values for the multiple comparisons (Crawley 2007).

Ethical note

This research was carried out under license from the Uganda National Council for Science and Technology (NS 234), and all procedures were approved by the Uganda Wildlife Authority. Trapping and marking procedures, which were part of the long term research programme, followed the guidelines of the Association for the Study of Animal Behaviour and are described in detail elsewhere (Cant 2000; Jordan et al. 2010).

Results

We found 15 call types related to different contexts within four main behavioural contexts (Table 1). The call types differed from each other in a range of temporal, frequency and waveform related parameters (Table 2 & 3). The discriminate function analysis (DFA) on 12 of the call types gave an overall cross-validated correct assignment (CV) of 39.6% (Wilks $\lambda = 0.011$, $F_{11} = 3.832$, $p > 0.001$). This is significantly higher then expected by change (8.3%, $p = 0.014$). The first discriminant function explained 37.6% of the variance.

Calls in the context of cohesion and movement

Close call system

The banded mongooses most frequently produced call type is the close call, potentially to maintain social organization during foraging. It is emitted almost continuously by all group members (excluding pups). In contrast to the contact or close calls of many other species, the close calls of the banded mongoose are not very stereotypic and contain some form of gradation (Figure 1). Messeri et al. (1987) already described this variation and concluded that banded mongoose have two close call (in that study contact call) types. In a recent study we concluded that the banded mongoose have one close call type, but the call type is graded and contains temporally separated vocal cues, expressing the callers' identity and its current behaviour as discrete units (Jansen et al. 2012).

Lead call

This multi-element call type was used by all adults and was usually given at the initiation of or during group movement. It has been shown that the call is involved in decision-making about initiation of group departure from their morning sleeping den (Furrer 2009), but is likely also involved in coordination of general group movement (Furrer 2009). The call generally consisted of two different elements (Figure 1b & 1c) . The first element was the close call as described under the close call system. The second element was a tonal element with variable frequency modulations and has either a low or high pitch. The most common order was 'close call'-'element' even though individuals occasionally produce calls with a different sequence length. Some of this flexibility in sequence lengths was also observed in the 'lost-' and 'excitement'-call (Chapter 3 for details). The call was also used by escorts of pups to stimulate the pups to follow them when moving between foraging patches.

Table 1. An overview of adult banded mongoose vocalisations sorted by behavioural context.

Call type	Description of context	Figure	Previous name(s)
	Cohesion/movement		
Close call	Frequently used contact call, potentially to maintain social organization during foraging.	1	Contact call
Lead call	Initiation and coordination of group movement.	1b & 1c	Moving call (Furrer 2009)
Lost call	Emitted by individuals separated from their natal group.	1d & 1f	–
	Resource calls		
Excitement call	Recruitment when encountering water or at onset of rain.	2a & 2b	'Water call' (Messeri et al. 1987)
Food growls	Calls in the context of foraging competition, likely to be graded with the aggression call.	2d	'Aggression call' (Messeri et al. 1987)
Food spits	Calls in the context of foraging competition, higher urgency then the food growl	2e	'Threat call' (Messeri et al. 1987)
Hunting call	Used when attempting to catch small mammals.		–
	Social calls		
Aggression	Used by both adults males and females when threatening others predominantly during eviction.	3f	–
Submission	During threat of eviction or after harassment both males and females emit this call.	3b3c	–
Screams	Produced during oestrus and harassment .	3d and 3e	'Distress call' (Messeri et al. 1987)
Mating call	Soliciting for mating.	3a	–
	Calls of context in danger		
Recruitment call	Calls produced in the context of group recruitment. in response to secondary predator cues, snakes and rival banded mongoose groups.	4a and 4b	'Rally call' (Messeri 1983; Messeri et al. 1987), 'War cry' (Müller and Manser 2008b), 'Screeching call' (Cant et al. 2002; Furrer et al. 2011)
Worry call	Graded alarm call system.	4d	–
Worried call		4e	–
Panic call	High urgency alarm call.	4f	–

Table 2. Acoustic parameters used in the discriminant function analyses.

Acoustic parameter	Location	Parameter category	Unit	Analysis[†]
Distance to max		Temporal	s	C, A
Fundamental frequency	Centre	Frequency	Hz	C
Fundamental frequency	Max	Frequency	Hz	C
Maximum frequency	Centre	Frequency	Hz	F
Frequency bandwidth	Centre	Frequency distribution	Hz	C, F
Max.frequency of quartile 75	Centre	Frequency distribution	Hz	C, F
Max.frequency of quartile 75	Max	Frequency distribution	Hz	C, A
Max.frequency of quartile 75	RSD*	Frequency distribution	Hz	C, F
Peak frequency	RSD*	Frequency distribution	Hz	C, A
Onset	Onset	Frequency modulation	Hz-	C, A
Maximum frequency step	-	Frequency modulation	Hz	C
HNR	Max		-	C,A
Entropy	Max		-	F
Peak amplitude	RSD*	Waveform	V	C ,F
Energy	-	Waveform	V^2s	C, A

[†] Letters in analysis column indicate which parameters were used in specific DFAs: C. Overall call types; and for testing the fit of the Morton's motivational structure rules based on levels of A. Aggression; and F. Fear

* Relative standard deviation

Table 3. Results of Kruskal-Wallis tests on single acoustic parameters.

Acoustical parameter	Location	Call types		Aggression		Fear	
		H^1	$p^{2,a}$	H^1	$p^{2,b}$	H^1	$p^{2,c}$
Duration	-	78.96	>0.001	39.84	>0.001		
Distance to max	-	42.35	> 0.001	17.62	0.007		
Fundamental freq.	Centre	56.44	>0.001			18.78	0.004
Fundamental frequency	Max	36.4	0.006	19.49	0.002		
Frequency bandwidth	Centre	41.48	0.001			21.56	0.001
Max .freq. of quartile 75	SD	34.78	0.011			23.67	>0.001
Mean frequency step	Mean	51.25	>0.001			14.64	0.03
Entropy	RSD*	38.16	0.003				
Peak amplitude	RSD*	31.10	0.044				
Energy	-	56.40	0.001	29.74	>0.001		

[1] H statistics from the Kruskal-Wallis test.

[2] The p values after a Holm–Bonferroni correction; [a] df = 11; [b]; df = 2; [c] df = 2.

* Relative standard deviation.

Lost call

Fairly regularly an individual mongoose became separated from its social group. Besides showing increased vigilance, these individuals generally emitted a specific vocalisation, the 'lost call' (Figure 1d- 1f). Upon hearing these calls, receiving

conspecifics often made their way towards the calling individual or actively searched for the caller. The exact function and the specific information receivers extracted from these calls remain to be tested. The call consisted of multiple elements of which the first was often the close call followed by one (Figure 1d) or more elements (Figure 1e) with a median of two elements. In some cases 'extremely' long sequences occurred (Figure 1f). The intensity of the call and the number of elements were likely to be effected by the level of arousal or fear experienced by the caller (Chapter 3). The call was only used by adults. Pups used their distress call when separated from their escort and/or social group (Figure 5c & Table 4).

Resource calls

Excitement call

This relatively high pitched multi-element vocalisation (Figure 2a & 2b) was mainly produced when mongooses encountered wet soil or at the on-set of rain. Call sequences generally consisted of the close call followed by a tonal element. The emission of the call results in recruitment of group members (Messeri et al. 1987). The call was mainly produced when multiple mongooses were already together and the call was not produced when encountering open water (Jansen 2009 personal observation). The previously suggested function of it being a 'water' call similar to 'food' calls in other species therefore seems to be unlikely. Why banded mongooses recruit group members to wet soil remains unclear. It might be linked maintaining group cohesion prior to the running for cover with onset of rain. Recruitment prior to running for cover could improve group cohesion and reduce group members getting separated from their social group.

Foraging competition

In the context of competition over food, two call types were used: growls (Figure 2d) and spits (Figure 2e). Calls occurred in a wide variety of intensity and duration, likely due to motivation of caller. Intense foraging competitions that, for example regularly occurred over large piles of elephant dung (*Loxodonta africana*), often lead to recruitment of group members (Rood 1975). Messeri et al. (1987) described two specific call types namely the 'threat' and 'aggression'. Threats are likely similar to our growls, whilst the aggression call is more like the spit call.

Hunting call

Banded mongooses occasionally 'hunted' for small rats or mice in thickets. Generally this was done by single individuals, but in rare cases multiple individuals

participated, although they did not seem to cooperate. During these 'hunting' events a special vocalisation was emitted (Figure 2f). In a typical situation an individual

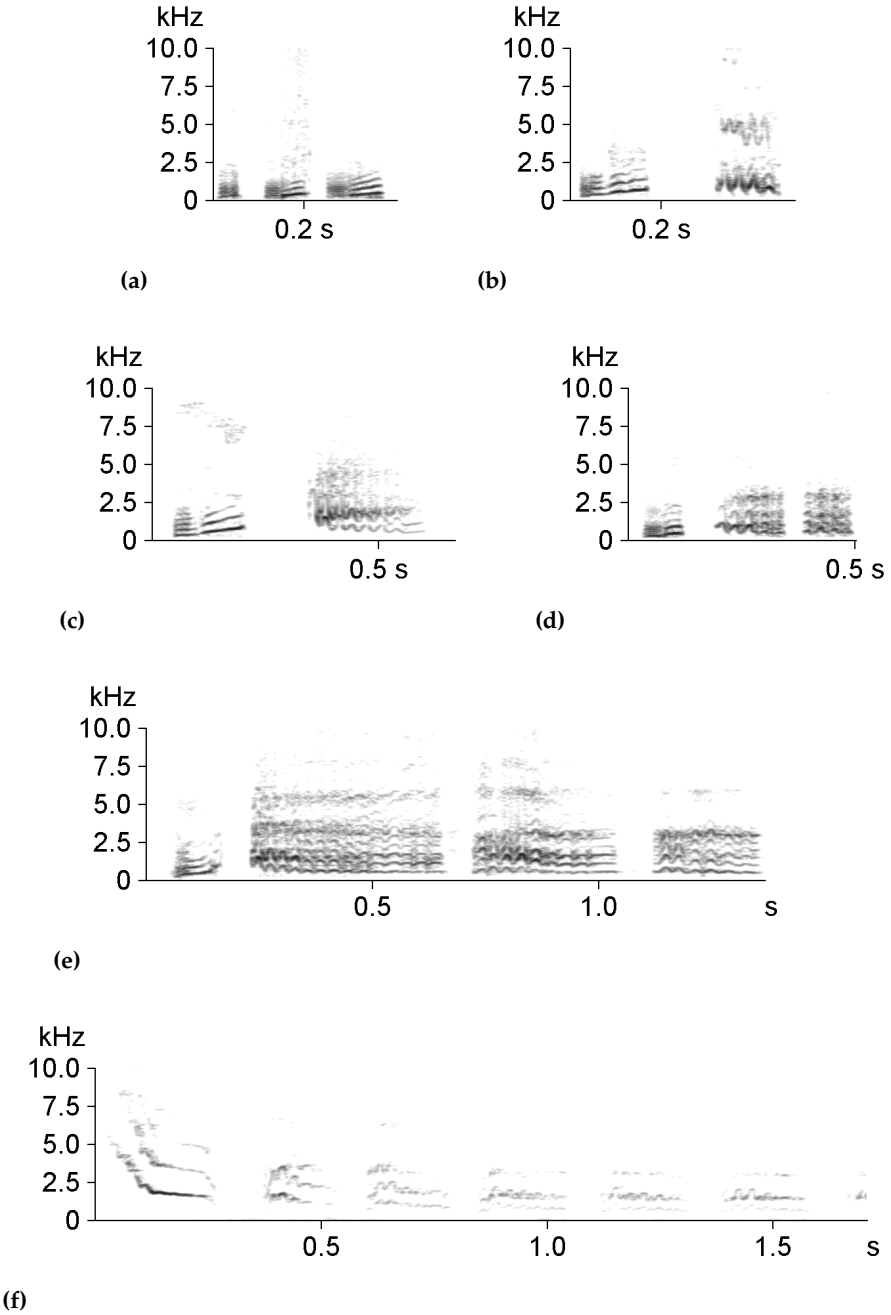

Figure 1. Typical calls examples in the context of group cohesion: a.) close calls; b.) lead call (low pitched); c.) lead calls (high pitched); d.) short series of lost calls; e.) long series of lost calls; and f.) series of lost call without preceding close call (Gauss, FTT=1024, overlap=97.87%, frequency resolution=43 Hz).

saw a rat run and disappear into a thicket. The mongoose then entered the ticket and produced this high pitched and noisy call. In some cases the rat responded by running away and it was then chased by the mongoose. If there was no response the call was repeated. In some cases several mongooses joined the 'hunt'. The caught rat was never shared. We did not record sufficient calls to be able to include them in the acoustical analysis.

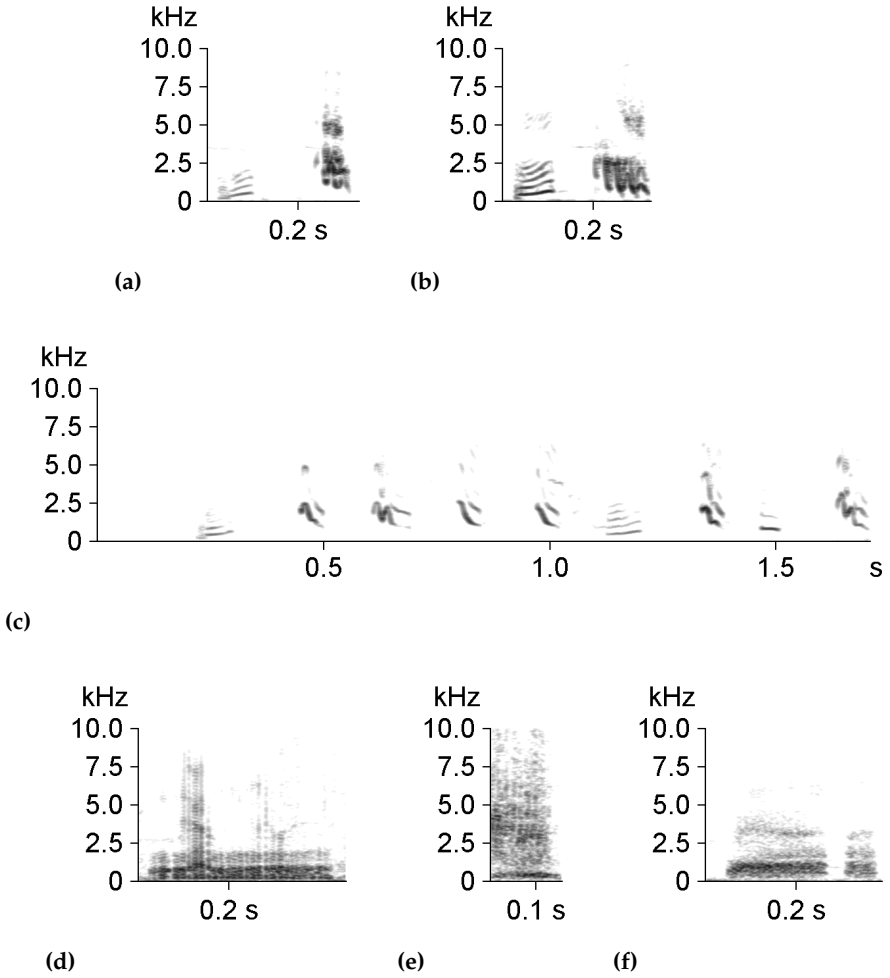

Figure 2. Typical examples of calls in the resource context: a. - c.) excitement calls; d.) food growl; e.) food spit; and f.) 'hunting' call (Gauss, FTT=1024, overlap=97.87%, frequency resolution=43 Hz).

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Social calls

Aggression call

Aggression calls were very variable in duration and intensity (Figure 3f). They were used by both adult males and females when threatening others predominantly during eviction. It was also by males to change pesters during mate guarding. It is possible that the food growls emitted in foraging competition were a low urgency version of this call type.

Submission call

This tonal call, emitted by adults and sub-adults of both sexes, was mainly produced after an individual experienced mild aggression or when under the threat of eviction, and the call was often accompanied with submissive or retreating behaviour (Figure 3b & 3c). This call was predominately used by young subordinate females in response to aggression by the dominant female(s).

Oestrus and harassment scream

Screams were loud harmonic calls with generally some frequency modulations (Figure 3d & 3e). The screams occurred in a range of context and intensities, but were always accompanied by physical aggression. During eviction screams became very loud and high pitched, in some cases going above the sensitivity of the microphone (+20 kHz). Messeri et al. (1987) noted a 'distress call' used by mongooses when caught by the experimenter. This might be the same vocalisation (at the higher end of intensity), but was not observed in that context, neither the described response of aggressive approach of group members towards the caller for assistance.

Mating call

Mating vocalisations (Figure 3a) were recorded in two instances and heard at least ones more during the field observations. Due to this small number of recordings, we were not able to include them in the acoustical analysis. Similar to observations in yellow mongoose (*Cynictis penicillata* LeRoux et al. 2009) recorded calls were associated with the soliciting of mating rather then mating itself.

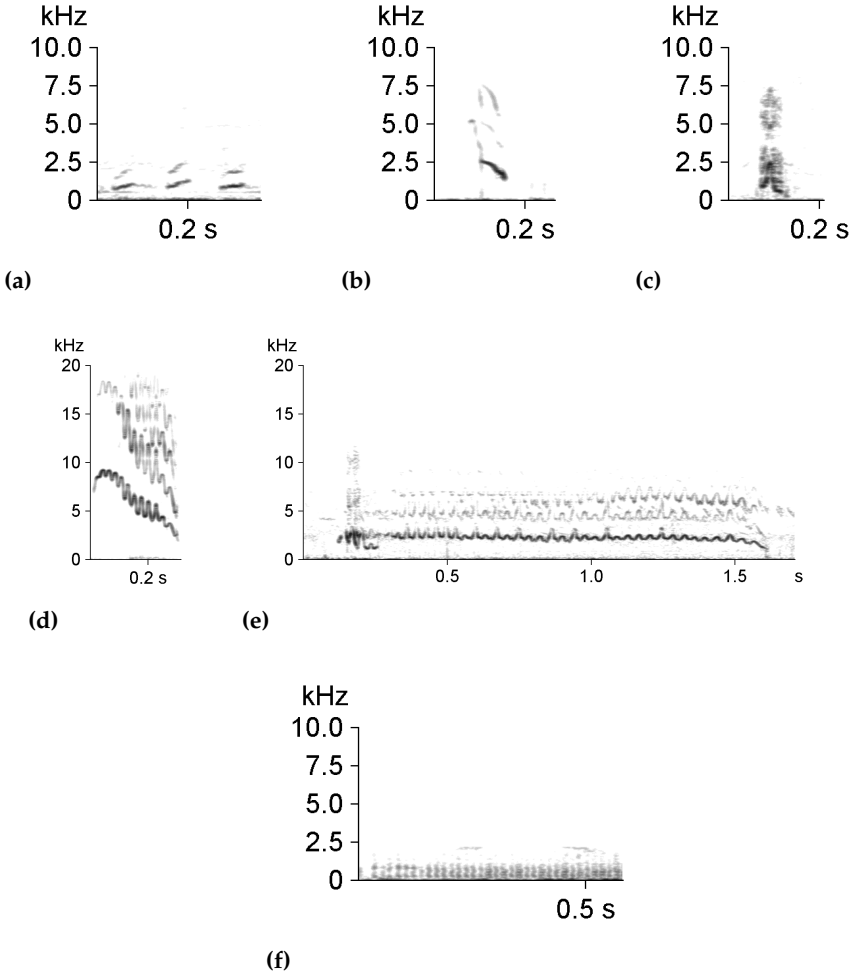

Figure 3. Typical examples of calls in the social context: a.) mating; b. - c.) submission; d. - e.) submission scream (note the different frequency scale); and f.) aggression growl. (Gauss, FTT=1024, overlap=97.87%, frequency resolution=43 Hz).

Calls in the context of danger

Recruitment calls (in the context of danger)

These calls are produced in the context of group recruitment to a range of different stimulus types: a.) secondary predator cues; b.) snakes; and c.) members of rival groups (Figure 4a & 4b, Furrer and Manser 2009). In response to snakes and rival groups a harsher variant is produced than in response to secondary predator cues. This suggests a graded rather than a discrete recruitment call system (Furrer and Manser 2009). Playbacks of calls elicited by the different stimuli cause individuals to approach the speaker, with receivers responding faster to the calls elicited by

snakes and rival mongooses, than to calls produced in response to faeces (Furrer and Manser 2009).

Alarm calls

In banded mongoose alarm calls have not been studied in detail, but it appears to be a graded urgency-based call system. Two to three different call types were observed, which are emitted in a wide range of contexts.

Worry and worried call Worry calls are harmonic calls that occurred singly or in sequences of multiple calls (Figure 4d). They were given in a wide variety of situations, such as overflying birds or prey, approaching humans, large herbivores and to secondary cues of other mongooses or of predators. It was a startle response to a sudden movement of the experimenter or a loud noise in the distance. Worried calls were of higher intensity and contained more noise 4e). Worried calls often contained multiple elements. Although worry and worried calls have been reported as distinct call types they are likely a graded system similar to the recruitment call. Animals briefly stopped foraging and showed increased vigilance in response to low intensity calls. In cases where the call was particularly intense, repeated over a long time and/or emitted by several callers instantaneously, the pack often ran for nearest cover and showed increased and prolonged vigilance. Likelihood of calling also depended on the presence of pups (pers. observation). For instance, mongooses would exclusively alarm to marabou stork (*Leptoptilos crumeniferus*) if pups were foraging with the group.

Panic call The panic call (Figure 4f) was only used in high urgency situations, uttered as a single and unrepeated vocalisations. This call type was for example used when a pack encountered a lion in a thicket. The call was loud, explosive and, in many cases, emitted by several pack members instantaneously. Therefore many recordings were clipped and/or merged. This resulted in insufficient good quality recordings to include this call type into the acoustical analysis. These calls elicited flight to nearest thicket, increased vigilance and in many cases was followed by repeated call bouts of worry or worried calls by multiple pack members.

Pup calls

In addition to the adult calls described here there were six specific types of pup vocalisations (Figure 5 & Table 4). These vocalisations were described in detail elsewhere (Metherell 2009). Messeri et al. (1987) merged all these into a single vocalisation the 'young call'.

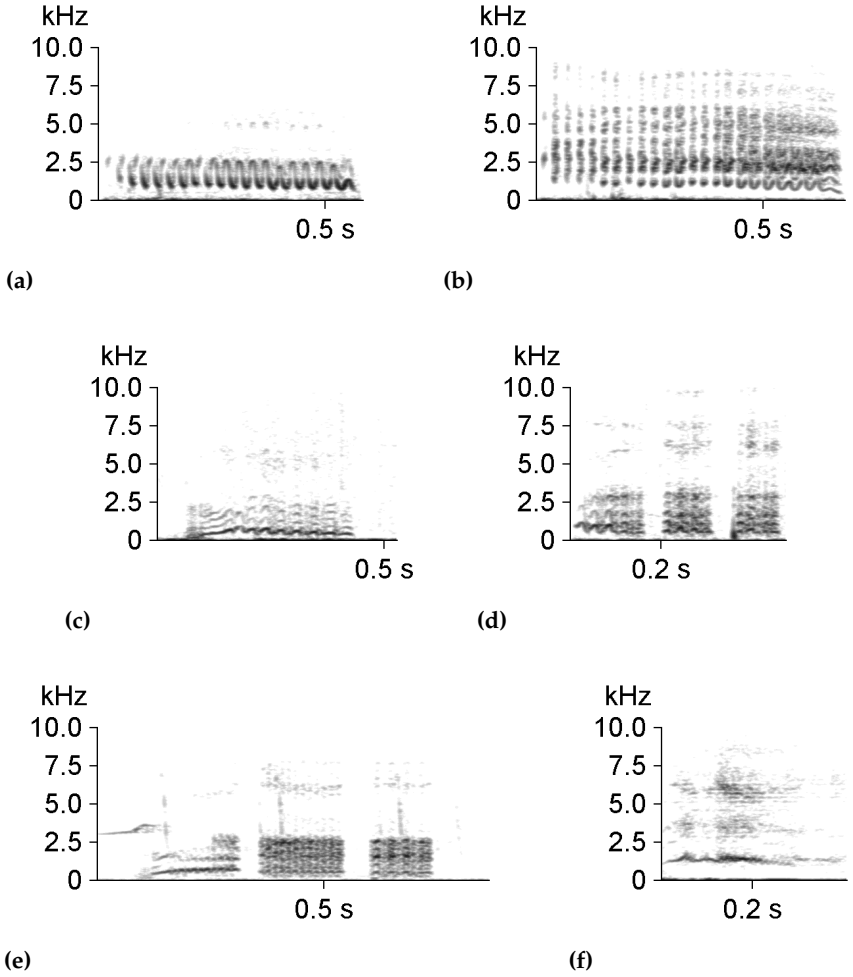

Figure 4. Typical example of calls in the context of danger: a.) low urgency recruitment; b.) high urgency recruitment; c.) alert; d.) worry; e.) worried; and f.) panic alarm calls (Gauss, FTT=1024, overlap=97.87%, frequency resolution=43 Hz).

Testing MS rules

Morton's MS rules predicted the relationship between the call structure and the context of vocalisations for a number of contexts (Table 5). The DFA based on the aggression categorises showed an overall cross-validated correct assignment (CV) of 75.5% (Wilks $\lambda = 0.450$, $F_7 = 6.794$, $p > 0.001$). This was significantly higher than expected by change (54.52%, $p = 0.004$). The first discriminant function explained 61.8% of the variance. Call types differed in both temporal and frequency aspects. Frequencies varied in distribution as well as in the degree of modulations. For the predictions based on fear an overall cross-validated correct assignment (CV) of 62.86% (Wilks $\lambda = 0.483$, $F_6 = 7.160$, $p = 0.001$). This was significantly

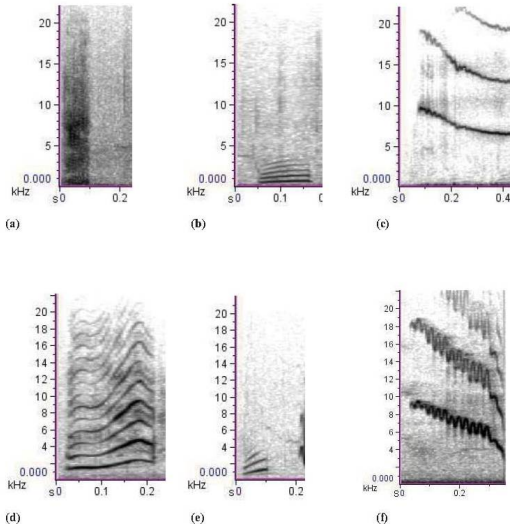

Figure 5. Examples of the six main call types emitted by pups; a.) aggressive; b.) digging; c.) distress; d) excitement; e.) moving; f.) begging (repeat) (Source: Metherell 2009, copied with permission).

Table 4. Overview of banded mongoose pup vocalisations.

Call type	Context
Begging/Repeat	Constantly emitted when closely following the escort
Aggressive	Defending a helper or food item from another pup
Digging	Pup is independently searching/digging for food
Distress	Separated from escort or group
Excitement	When adult is seen or approached with a food item
Moving	When moving quickly or running

Call classification is based on Metherell 2009

higher than expected by chance (35.26%, $p = 0.042$). The first discriminant function explained 83.1% of the variance. Call types differed in both temporal and frequency aspects. Frequencies varied in distribution as well as in the degree of modulations (Table 2 & 3) .

In banded mongooses increased levels of aggression showed a higher mean 75% quartile frequency. The mean fundamental frequency was the highest in mild situations of aggression and lowest in the no aggression context). A similar pattern (i.e. no → fully → mild aggression) was observed for the duration of the call. This occurred in different behavioural context in call types such as aggression calls, food growls and recruitment calls. Low aggressive interactions correlated to calls that

were of a narrow frequency range, while highly aggressive situations correlated to calls with a noisy broad band (see Furrer and Manser 2009, for detailed decription in recruitement calls). In the context of fear we observed an increase in fundamental frequency, bandwidth and mean frequency step, whilst the RSD of the 75% quartile was reduced. These parameters indicated that the call became higher pitched, contained more noise and showed an increase in frequency modulations the more fear an individual experienced.

Table 5. Overview of Morton's motivational structure rules categories for adult banded mongoose vocalisations.

Call type	Frequency	Tonality	MS rules Prediction *	Fit
	Cohesion/movement			
Close call	Low	Tonal/noisy parts	NN	–
Lead call†	Medium	Tonal	NN	–
Lost call†	Medium	Tonal	FN	yes (fear)
	Resourse calls			
Excitement†	Medium to High	Tonal	NN	–
Food growls	Low	Noisy	NM	yes (aggression)
Food spits	Medium to High	Noisy	NF	partly (aggression)
Hunting call	Low	Noisy	NN or NM	yes (aggression)
	Social calls			
Aggression	Low	Noisy	LF	yes (aggression)
Submission	Medium to Low	Tonal	FN or SN	yes (fear)
Screams	High	Tonal	FN or FM	yes (fear)
Mating call	Low	Tonal	NN	–
	Calls of context in danger			
Recruitment	Medium	Tonal/noisy parts	SM or FF	partly (aggression)
Worry call	Medium	Tonal/noisy parts	FN	
Worried call	Medium	Ton/noisy parts	SN	yes (fear)
Panic call	High	Noisy	FN	

† Looking at the additional element

* Morton's structural rule category based on i.) level of fear: (N = no fear, S = suspicious, F= fearful); and ii.) level of aggressiveness (N = no aggression, M = medium aggression, F = fully aggressive)

Discussion

Adult banded mongoose in their natural habitat used at least 15 call types associated with different behavioural contexts or external events (Table 1). In addition six specific pup vocalisation call types have been described (Table 4; Metherell 2009).

Many of the banded mongoose call types showed considerable variation in multiple acoustic parameters, such as duration, fundamental frequency, noisiness and tonality. The graded nature of the vocal repertoire complicated the categorisation in number of call types (Hammerschmidt and Fischer 1998). For instance, it was difficult to decide if calls such as 'food growls' versus 'aggression calls', 'submission calls' versus 'harassment screams' and 'worry' versus 'worried' alarm calls were acoustically discrete call types or if they should be considered as single call types with a graded structure. We identified some differences with the banded mongoose vocal repertoire described for a captive population (Messeri et al. 1987) and found some previously not reported call types.

Generally arousal, valence and potency effects will alter vocalisations and are likely linked to levels of perceived aggression and fear (Morton 1977; Goudbeek and Scherer 2010; Briefer 2012). The increase of noise and reduced fundamental frequency of vocalisations with elevated levels of aggressiveness was, for instance, found in the recruitment call (Figure 4a & 4b). The calls graded from tonal and low pitched in low urgency threat situations (e.g. secondary predator cues) to harsher, noisier and higher pitched in high urgency threat/danger situations (Furrer and Manser 2009). The highest urgency of the recruitment call (also referred to as 'warcry') is used in inter-group encounters, which are highly aggressive interactions (Cant et al. 2002; Furrer and Manser 2009). A congruent tendency of increased noise and reduced pitch with increased aggression was observed in food growls (Figure 2d) or aggression growls (Figure 3f). Increased levels of urgency did not show the predicted increase of fundamental frequency in recruitment calls. It is, however, possible that mongooses do not undergo an increased level of fear *per se* with increased urgency in the context of recruitment. On the fear axes, intensity and increased pitch of lost calls seemed to be linked to duration of being lost ($\approx$ increased fear; Jansen pers. observation). Screams of victims of aggression (e.g. during eviction) also increased in intensity and pitch related to the levels of received aggression and severity of injury, thereby likely increased fear. Females that were under threat of eviction and received high levels of aggression emitted screams that were sometimes extremely high pitched ($\leq$ 20 kHz) and additionally showed considerable variation in duration, frequency sweeps and frequency modulations.

Call types such as the lost call and the recruitment calls showed a high frequency modulation, and a strong down sweep in many of the call types. Morton (1977) predicted a frequency modulation in fundamental frequencies in the medium aggression content, but we observed these drops in a wider range of contexts and the drops were stronger than 'expected'. These frequency modulations were not explicitly measured in this study, but several of the measurements can be seen as

indicators for the high variability of the peak frequency within the call (i.e the various relative standard deviation of peak frequency, onset and maximum frequency step; Table 2 & 3).

Even though the concept of graded versus discrete vocalisations recently has justly been criticised (Bouchet et al. 2012; Keenan et al. 2013), it remains clear that vocal repertoires differ in the degree of gradedness/discreteness. The evolution of graded versus discrete call systems had been linked to the interplay of habitat and social systems, where sociable species inhabiting open habitats should evolve graded vocal repertoires (Marler 1976). This is partly true for the banded mongoose, which are both social and have many close distance interactions. However compared to the habitat of the meerkat the habitat in our study site was more densely vegetated. However, linked to these differences in habitat is predation as a factor that has hypothesised to play a role in the evolution of a species' call system. Predation or rather variations in predator-specific avoidance strategies, affect the alarm call systems, where species with multiple escape strategies are predicted to evolve discrete systems (Macedonia and Evans 1993; Furrer 2009). The results by Furrer and Manser (2009) suggested a graded rather than a discrete recruitment call system. Behavioural observations suggest a similar situation in the alarm calls. The absence of the sentinel behaviour in banded mongooses in comparison to dwarf mongoose (Rasa 1986) and meerkats (Clutton-Brock et al. 1999) is likely also linked to these differences in habitat. It is likely that the selective pressures on various aspects of the call repertoire (i.e. affiliative versus alarm calls) are different and this may explain the intermediate systems observed in many species.

Conclusion

The data in this paper adds to the data on vocal repertoires of mongoose species. We show that banded mongooses use at least 15 different call types in relation to cohesion/movement, resources, social interactions and danger. Behavioural observations suggest that graded variations in factors such as intensity and duration are linked to the caller's motivational state and that they fit some of the MS rule predictions. More detailed behavioural observations and playback experiments will be needed to establish how meaningful these differences within and between call types are. At present it is unclear why the banded mongoose would have evolved a rather graded vocal repertoire, whilst similar species such as the meerkat and dwarf mongoose have a more discrete vocal repertoire. Some of these differences are likely an interplay between social and environmental factors.

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References

Agnarsson, I, M Kuntner, and LJ May-Collado (2010). "Dogs, cats, and kin: A molecular species-level phylogeny of Carnivora". *Molecular Phylogenetics and Evolution*, 54(3), 726–745.

Altman, J (1974). "Observational study of behavior: sampling methods". *Behaviour*, 49, 227–267.

Bates, DM (2011). *lme4: Mixed-effects modeling with R*. New York: Springer.

Blumstein, DT and KB Armitage (1997). "Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls". *American Naturalist*, 150(2), 179–200.

Bouchet, H et al. (2012). "Acoustic variability and indvidual distictiveness in the vocal repertoire of red-capped mangabeys (Cercocebus torquatus)". *Journal of Comparative Psychology*, 126(1), 45–56.

Briefer, EF (2012). "Vocal expression of emotions in mammals: mechanisms of production and evidence". *Journal of Zoology*, 288(1), 1–20.

Cant, MA (1998). "Communal breeding in banded mongooses and the theory of reproductive skew". PhD thesis. Cambridge, UK: University of Cambridge.

— (2000). "Social control of reproduction in banded mongooses". *Animal Behaviour*, 59(1), 147–158.

— (2003). "Patterns of helping effort in co-operatively breeding banded mongooses *Mungos mungo*". *Journal of Zoology*, 259(2), 115–121.

Cant, MA, E Otali, and F Mwanguhya (2002). "Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose". *Ethology*, 108(6), 541–555.

Cant, MA et al. (2010). "Reproductive control via eviction (but not the threat of eviction) in banded mongooses". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 277(1691), 2219–2226.

Charrier, I, T Aubin, and Mathevon (2010). "Mother-Calf vocal communication in Atlantic walrus: a first field experiment". *Animal Cognition*, 13(3), 471–482.

Clutton-Brock, TH et al. (1999). "Selfish sentinels in cooperative mammals". *Science*, 284(5420), 1640–1644.

Crawley, MJ (2007). *The R book*. Chichester: John Wiley & Sons.

De Luca, DW and JR Ginsberg (2001). "Dominance, reproduction and survival in banded mongooses: towards an egalitarian social system?" *Animal Behaviour*, 61(1), 17–30.

Ey, E and J Fischer (2009). "The acoustic adaptation hypothesis - a review of the evidence from birds, anurans and mammals". *Bioacoustics*, 19(1-2), 21–48.

Fitch, WT (2000). "Skull dimensions in relation to body size in nonhuman primates: the causal bases for acoustic allometry." *Zoology*, 103(1-2), 40–58.

Freeberg, TM, RIM Dunbar, and TJ Ord (2012a). "Social complexity as a proximate and ultimate factor in communicative complexity". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1785–1801.

Freeberg, TM, TJ Ord, and RIM Dunbar (2012b). "The social network and communicative complexity: preface to theme issue". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1782–1784.

Furrer, RD (2009). "Leadership and group-decision-making in banded mongooses (*Mungos mungo*)". PhD thesis. Zurich, Switzerland: University of Zurich.

Furrer, RD and MB Manser (2009). "Banded mongoose recruitment calls convey information about risk and not stimulus type". *Animal Behaviour*, 78(1), 195–201.

Furrer, RD et al. (2011). "Location and group size influence decisions in simulated intergroup encounters in banded mongooses". *Behavioral Ecology*, 22(3), 493–500.

Gilchrist, JS and E Otali (2002). "The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose". *Canadian journal of Zoology*, 80(10), 1795–1802.

Goudbeek, M and K Scherer (2010). "Beyond arousal: Valence and potency/control cues in the vocal expression of emotion". *Journal of the Acoustical Society of America*, 128(3), 1322:1336.

Green, S (1975). "Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study". *Primate Behavior, Developments in Field and Laboratory Research*, 2, 1–102.

Gusset, M (2007). "Banded together: a review of the factors favouring group living in a social carnivore, the banded mongoose *Mungos mungo* (Carnivora: *Herpestidae*)". *Mammalia*, 71, 80–82.

Hammerschmidt, K and J Fischer (1998). "The Vocal Repertoire of Barbary Macaques: A Quantitative Analysis of a Graded Signal System." *Ethology*, 104(3), 203–216.

Hauser, MD (1996). *The evolution of communication*. Cambridge, MA: MIT Press.

— (1998). "Functional referents and acoustic similarity: field playback experiments with rhesus monkeys". *Animal Behaviour*, 55(6), 1647–1658.

Heiberger, RM and B Holland (2004). *Statistical Analysis and Data Display: An Intermediate Course with Examples in S-Plus, R, and SAS*. Springer Texts in Statistics.

Heiberger, RM (2012). *HH: Statistical Analysis and Data Display: Heiberger and Holland*. R package version 2.3-27.

Jansen, DAWAM, MA Cant, and MB Manser (2012). "Segmental concatenation of individual signatures and context cues in banded mongoose *Mungos mungo* close calls". *BMC Biology*, 10(97).

Jordan, NR et al. (2010). "Scent marking within and between groups of wild banded mongooses". *Journal of Zoology*, 280(1), 72–83.

Keenan, S, A Lemasson, and K Zuberbühler (2013). "Graded or discrete? A quantitive analyis of Campbell's monkey alarm calls". *Animal behaviour*, 85(1), 109–118.

Le Roux, A, MI Cherry, and MB Manser (2008). "The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*". *Animal Behaviour*, 75(3), 943–949.

LeRoux, A, MI Cherry, and MB Manser (2009). "The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality". *Naturwissenschaften*, 96(5), 575–584.

Macedonia, JM and CS Evans (1993). "Variation among mammalian alarm call systems and the problem of meaning in animal signals". *Ethology*, 93(3), 177–197.

Manser, MB (1998). "The evolution of auditory communication in suricates, *Suricata suricatta*". PhD thesis. Cambridge, UK: University of Cambridge.

— (2001). "The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268(1483), 2315–2324.

— (2010). "The generation of functionally referential and motivational vocal signals in mammals". In: *Handbook of mammalian vocalization*. Ed. by S Brudzynski. New York: Elsevier, pp. 495–503.

Marler, P (1967). "Animal Communication Signals". *Science*, 157(3790), 769–774.

— (1975). "On the origin of speech from animal sounds." In: *The role of speech in language*. Ed. by J Kavanagh and J Cutting. Cambridge, MA: MIT Press. Chap. On the origin of speech from animal sound, pp. 11–37.

— (1976). "Social organization, communication and graded signals the chimpanzee and the gorilla". In: *Growing points in ethology*. Ed. by PPG Bateson and RA Hinde. Cambridge: Cambridge University Press, pp. 239–281.

Marler, P (1977). "The evolution of communication". In: *How animals communicate*. Ed. by TA Sebeok. Bloomington: Indiana University Press, pp. 45–70.

Marler, P and PC Mundinger (1975). "Vocalizations, social-organization and breeding biology of twite *Acanthus flavirostris*". *Ibis*, 117, 1–6.

Masi, E et al. (1987). "Some Aspects of the Vocal Repertoire of the Banded Mongoose, *Mungos mungo*". *Italian journal of Zoology*, 21(2), 193–194.

McComb, K and S Semple (2005). "Co-evolution of vocal communication and sociality in primates". *Biology Letters*, 1(4), 381–385.

Messeri, P (1983). "A preliminary comparison between social behaviors of 2 viverrids, the dwarf mongoose and the banded mongoose, in Somalia". *Italian journal of Zoology*, 17(2), 200–200.

Messeri, P et al. (1987). "A study of the vocal repetoire of the banded mongoose (*Mungos mungo*)". *Italian journal of Zoology*, 19(22), 341–73.

Metherell, B (2009). "Offspring care and communication in the banded mongoose". PhD thesis. Cambridge, UK: University of Cambridge.

Morton, ES (1975). "Ecological sources of selection on avian sounds". *American Naturalist*, 109(965), 17–34.

— (1977). "Occurance and significance of motivation structural rules in some bird and mammal sounds". *American Naturalist*, 111(981), 855–869.

— (1982). "Grading, discreteness, redundancy, and motivation-structural rules." In: *Acoustic Communication in Birds*. Ed. by D Kroodsma and E Miller. Vol. 1. New York: Academic Press, 183–212.

Müller, CA and MB Manser (2008a). "Mutual recognition of pups and providers in the cooperatively breeding banded mongoose". *Animal Behaviour*, 75(5), 1683–1692.

— (2008b). "Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew". *Ethology*, 114(2), 174–185.

Mundry, R and C Sommer (2007). "Discriminant function analysis with nonindependent data: consequences and an alternative". *Animal Behaviour*, 74(4), 965–976.

Nichols, HJ et al. (2010). "Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose". *Animal Behaviour*, 80(4), 649–657.

Ord, TJ and J Garcia-Porta (2012). "Is sociality required for the evolution of communicative complexity? Evidence weighed against alternative hypotheses in diverse taxonomic groups". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1811–1828.

R Core Team (2012). *R: A Language and Environment for Statistical Computing*. ISBN 3-900051-07-0. R Foundation for Statistical Computing. Vienna, Austria.

Range, F and J Fischer (2004). "Vocal Repertoire of Sooty Mangabeys (*Cercocebus torquatus atys*) in the Taï National Park". *Ethology*, 110(4), 301–321.

Rasa, OAE (1986). "Coordinated Vigilance in Dwarf Mongoose Family Groups: The 'Watchman's Song' Hypothesis and the Costs of Guarding". *Ethology*, 71(4), 340–344.

Rood, JP (1974). "Banded Mongoose Males Guard Young". *Nature*, 248(5444), 176–176.

— (1975). "Population dynamics and food habits of the banded mongoose". *East Africa Wildlife journal*, 13, 89–111.

Schrader, L and K Hammerschmidt (1997). "Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach." *Bioacoustics*, 7(4), 247–265.

Specht, R (2012). *Avisoft SASLab Pro. User's Guide for version 5.2*. Avisoft Bioacoustics. Berlin.

Venables, WN and BD Ripley (2002). *Modern Applied Statistics with S*. 4th. Berlin Heidelberg: Springer.

Veron, G et al. (2004). "Molecular systematics and origin of sociality in mongooses (*Herpestidae*, Carnivora)". *Molecular Phylogenetics and Evolution*, 30(3), 582–598.

Weihs, C et al. (2005). "klaR Analyzing German Business Cycles". In: *Data analysis and decision support*. Ed. by D Baier, R Decker, and L Schmidt-Thieme. Berlin: Springer, pp. 335–343.

2

Segmental concatenation of individual signatures and context cues in banded mongoose close calls

David A.W.A.M. Jansen, Michael A. Cant and Marta B. Manser. (2012) Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls calls. *BMC BIOLOGY*, 10(97)

Segmental concatenation of individual signatures and context cues in banded mongoose close calls

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Abstract

Background
All animals are anatomically constrained in the number of discrete call types they can produce. Recent studies suggest that by combining existing calls into meaningful sequences, animals can increase the information content of their vocal repertoire despite these constraints. Additionally, signallers can use vocal signatures or cues correlated to other individual traits or contexts to increase the information encoded in their vocalizations. However, encoding multiple vocal signatures or cues using the same components of vocalizations usually reduces the signals' reliability. Segregation of information could effectively circumvent this trade-off. In this study we investigate how banded mongooses (*Mungos mungo*) encode multiple vocal signatures or cues in their frequently emitted graded single syllable close calls.

Results
The data for this study were collected on a wild, but habituated, population of banded mongooses. Using behavioural observations and acoustical analysis we found that close calls contain two acoustically different segments. The first being stable and individually distinct, and the second being graded and correlating with the current behaviour of the individual, whether it is digging, searching or moving. This provides evidence of Marler's hypothesis on temporal segregation of information within a single syllable call type. Additionally, our work represents an example of an identity cue integrated as a discrete segment within a single call that is independent from context. This likely functions to avoid ambiguity between individuals or receivers having to keep track of several context-specific identity cues.

Conclusions
Our study provides the first evidence of segmental concatenation of information within a single syllable in non-human vocalizations. By reviewing descriptions of call structures in the literature, we suggest a general application of this mechanism. Our study indicates that temporal segregation and segmental concatenation of vocal signatures or cues is likely a common, but so far neglected, dimension of information coding in animal vocal communication. We argue that temporal segregation of vocal signatures and cues evolves in species where communication of multiple unambiguous signals is crucial, but is limited by the number of call types produced.

Keywords: vocal signature, vocal cue, syllable, close call, segregation of information, graded calls, banded mongoose, segmental concatenation

Background

Nonhuman-animals (hereafter referred to as animals) have finite vocal repertoires and are anatomically constrained in the number of different call types they can produce (Fitch 2000; Hammerschmidt and Fischer 2008). These constraints limit the variation of a species' vocal repertoire and may have played an important role in the evolution of meaningful combinations of calls (Arnold and Zuberbühler 2006; Arnold and Zuberbühler 2008). Another possible way to encode senders' related information in vocalizations is through vocal signatures (specifically for individual identity and/or group membership) and/or cues (related to all other individual traits or context; hereafter we refer to both signatures and cues as vocal cues; Hauser 1996; Bradbury and Vehrencamp 1998; Maynard-Smith and Harper 2003; Shapiro 2010).

Although individual identity is the most commonly reported vocal cue (Shapiro 2010), animal vocalizations have also been shown to contain cues for group identity (Boughman and Wilkinson 1998; Crockford et al. 2004; Briefer et al. 2008; Shapiro 2010; Townsend et al. 2010), size (Fitch 1997; Reby and McComb 2003; Vannoni and McElligott 2008), male quality, (Clutton-Brock and Albon 1979; Reby and McComb 2003; Fischer et al. 2004), sex (Charlton et al. 2009; Mathevon et al. 2010), and reproductive state (Charlton et al. 2010). Animals can encode vocal cue information using two general sets of acoustic properties. Firstly, spectral features, such as fundamental frequency or harmonic-to-noise ratio, can differ between individuals to encode for instance individuality (Shapiro 2010). Additionally, a number of recent studies have shown that filter-related formants are a reliable indication of body size and male quality (Fitch 1997; Riede and Fitch 1999; Reby and McComb 2003; Vannoni and McElligott 2008). The importance of these formants has mainly been shown in larger mammals, such as rhesus macaques (*Macaca mulatta*; Fitch 1997), dogs (*Canis familiaris*), red deer (*Cervus elaphus*; Reby et al. 1998; Reby and McComb 2003) or fallow deer (*Dama dama*; Vannoni and McElligott 2008). Secondly, vocal cue information can be encoded in vocalizations through temporal features. Individual cues encoded by variance in the temporal features, such as duration or temporal arrangement of frequency elements have been reported for species such as the big brown bat (*Eptesicus fuscus*), pallid bat (*Antrozous pallidus*), and cricket species (*Gryllidae spp.*; Shapiro 2010). All of these vocal cues potentially provide useful information to the receiver whenever variation between categories is larger than the within-category variation. Many animal calls contain combinations of multiple different vocal cue types (Hauser 1996; Bradbury and Vehrencamp 1998; Maynard-Smith and Harper 2003; Shapiro 2010). The expression of these multiple

vocal cues typically correlates with different frequency-related acoustic parameters. The individualistic grunts of baboons (*Papio spp.*) are, for instance, audibly distinct in different behavioural contexts (Owren et al. 1997; Rendall et al. 1999; Rendall 2003). However, acoustic space is limited and many acoustic parameters are correlated with one another. Therefore, the amount of frequency related variation that can be used by signallers to encode different vocal cues is ultimately constrained. This constraint can result in a trade-off between the various kinds of information and typically reduces reliability of at least one of the vocal cues (Marler 1960; Briefer et al. 2010). For instance, the use by signallers of available variation for individual recognition conflicts with the need for stereotypic characteristics for group recognition in bird song (Marler 1960). Briefer et al. (2010) showed a similar trade-off between the vocal cues for identity (stable over time) and male quality (variable over time) in fallow deer.

Segregation of information could partially resolve this trade-off by expressing functionally different cues in temporally distinct call segments or in different acoustic features (Marler 1960; Briefer et al. 2010). In the white-crowned sparrow (*Zonotrichia leucophrys pugetensis*), for example, individual identity and group membership are segregated into the distinct note complex and trill phrases of its song respectively, thus avoiding a trade-off in reliability between the vocal cues (Nelson and Poesel 2007). Similar segregation of information (though not specifically referred to) has been shown in the songs of meadow pipits (*Anthus pratensis*; Elfstörm 1990), rock hyraxes (*Procavia capensis*; Koren and Geffen 2009), humpback whales (*Megaptera novaeangliae*; Payne and McVay 1971) and killer whales (*Orcinus orca*; Ford 1989). Although this principle was proposed by Marler in 1960 (Marler 1960), currently no studies have shown temporal segregation in the form of segmental concatenation within a single syllable call type. Such within-syllable encoding would have analogues with 'phonological' or segmental concatenation used in human language (Hauser and Fitch 2003).

Contact calls are among the most common vocalizations produced by both mammalian and bird species. In a variety of species, contact calls seem to function to coordinate movements and cohesion of individuals on a range of spatial scales, concurrently with various behaviours and in a variety of social systems (DaCunha and Byrne 2008; Kondo and Watanabe 2009). Contact calls have been shown to contain individual vocal cues (Janik et al. 1994; Shapiro 2010; Townsend et al. 2010) and group membership vocal cues (Boughman and Wilkinson 1998; Briefer et al. 2008; Jameson and Hare 2009; Townsend et al. 2010). Contact calls can also contain multiple vocal cues as has been shown in baboons (Owren et al. 1997; Rendall et al. 1999; Rendall 2003) and meerkats (*Suricata suricatta*; Townsend et al. 2010).

In some species contact calls seem to function predominantly over mid- to long-distance, while in others contact calls play a more important role in short-distance communication. It has been suggested that these short distance close calls, often low in amplitude and pitch and consisting of a single syllable, are better described as close calls (Harcourt et al. 1993; Townsend et al. 2010). Such close calls have the potential to provide constant information about the individual characteristics of the signaler and are likely used to monitor changes in behaviour and relative spatial positioning of members in social groups (DaCunha and Byrne 2008; Kondo and Watanabe 2009; Townsend et al. 2010; Townsend et al. 2011; Townsend et al. 2012).

Cooperatively breeding banded mongooses (*Mungos mungo*) are small (≤ 2kg) social carnivores that show high group cohesion. They live in mixed sex groups, with an average of around 20 individuals, but groups occasionally grow to more than 70 individuals (Cant 1998). They forage together as cohesive units and cooperate in pup care, predator avoidance and territory defence (Rood 1975; Cant 1998; Cant 2000). During foraging, banded mongooses move in and out of dense vegetation with many position shifts, both in distance to nearest neighbour and in relative position within the group. They regularly dig for food items in the soil with their heads down. Besides digging they also search for food on the surface, but this is mainly done in the thickets (see Table 1 for details). They are often visually constrained during foraging and, therefore vocalizations play a critical role in keeping individuals informed of changes in the social and ecological environment. Banded mongoose use a range of graded vocalizations to coordinate behaviours and to maintain group cohesion (Messeri et al. 1987; Furrer 2009). One of the most commonly emitted call types is the close call and previous work has demonstrated the presence of an individual vocal cue within the call (Müller and Manser 2008). Subsequent field observations suggested additional graded variation in the close calls, which appeared to be related to the behavioural context experienced by the signaler (personal observations DJ). We, therefore, investigated whether banded mongooses' close calls contain multiple vocal cues and how these vocal cues are encoded in the temporal and frequency related aspects of this graded single syllable call type.

Results

The acoustic structure of close call in banded mongoose varied significantly between individuals and behavioural contexts. Specifically, the initial noisy segment of the call remained stable within an individual in all of the quantified behavioural contexts, while a gradation was detected in the subsequent harmonic tonal segment

Table 1. Definitions of the different behavioural context used for the acoustical analysis.

Context	Definition
Digging	The signaler was digging for or eating food, and the animal was not moving and its head was facing downward.
Searching	The signaler was searching for food in and around the same foraging patch, with head predominately facing downward.
Moving	The signaler was moving between foraging patches but within the spatial cohesion of the group and with head predominately facing forward.

(Table 1). Close calls could be individually distinguished statistically in all four groups (total number of individuals = 36, range per group 7 to 14). Correct cross validation probabilities varied between 40% and 61% for the initial noisy segment and the whole call, and bootstrapping showed that all classification probabilities were much higher than that expected by chance (Table 2). The cross-validation probabilities for the harmonic part of the call were considerably lower at 11% to 25% and were not significantly different than expected by chance (Table 2. A group-specific vocal cue was found in the noisy segment of the call (number of correctly cross-classified elements $(ncce) = 44.47$, $P = 0.038$, $n = 36$), but not for the whole call ($ncce = 38.08$, $P = 0.27$), nor for the harmonic segment ($ncce = 44.47$, $P = 0.038$, $n = 36$). No evidence for a sex-specific vocal cue was found in either the whole call ($ncce = 60.35$, $P = 0.54$, $n = 36$), or the initial noisy part ($ncce = 64.23$, $P = 0.19$, $n = 36$).

A cross-classified permutated discriminant function analysis (pDFA) showed that, overall, close calls were correctly classified to the appropriate behavioural context (Table 1) based on their acoustic structure ($ncce = 44.22$, $P < 0.001$, $n = 20$). Specifically, the harmonic extension of the close calls varied significantly and was correctly classified according to the behavioural context ($ncce = 78.04$, $P = 0.009$, $n = 18$), whereas the initial noisy segment of the call was not ($ncce = 19.87$, $P = 0.79$, $n = 20$). Thereby, the harmonic segment was either not present or of a very short duration in the digging context ($mean \pm sd$; 0.01 ± 0.02s), while its duration increased in the searching context (0.05 ± 0.03s). The longest and most pronounced harmonic segments were observed in the moving context (0.08 ± 0.03s). For pairwise comparisons of the acoustic structures between behavioural contexts, see Table 3.

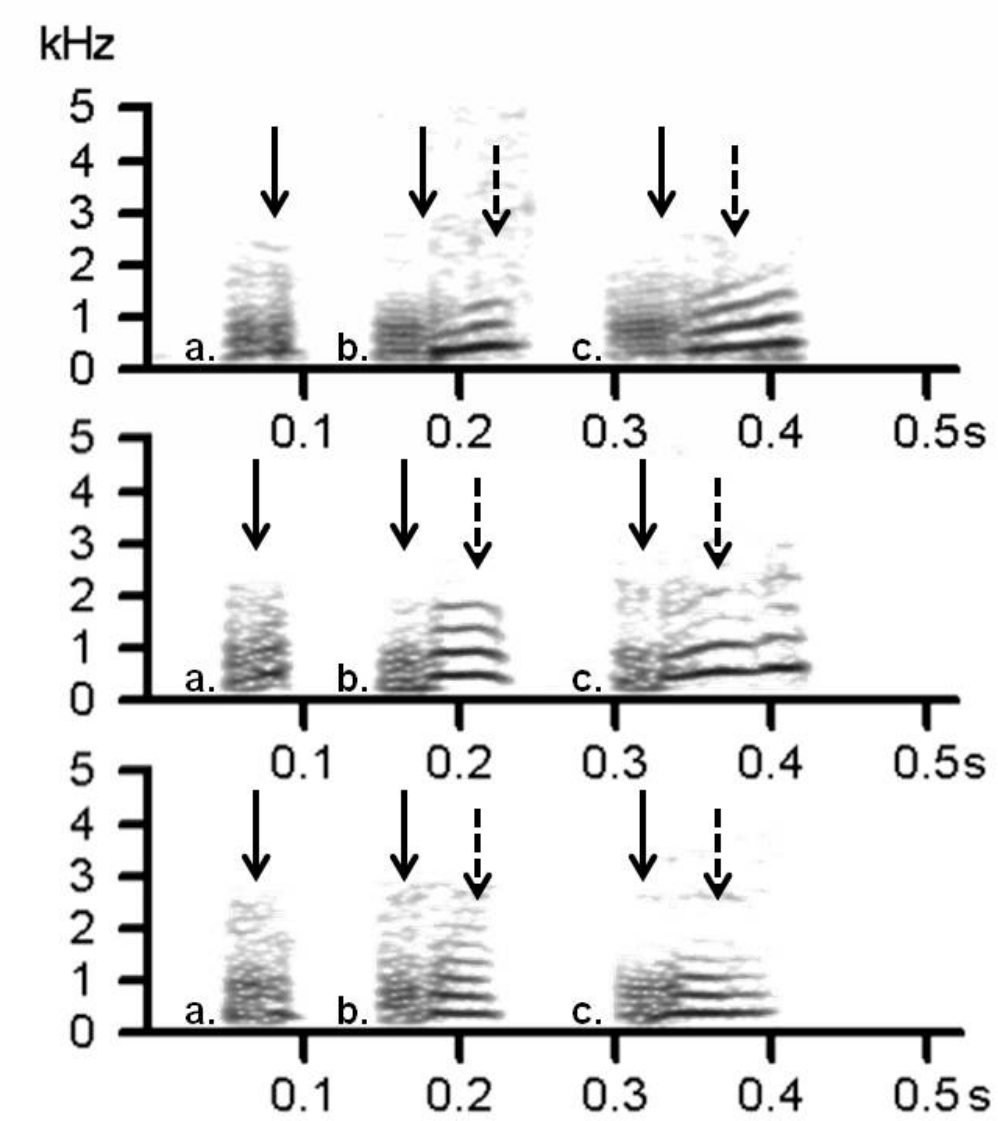

Figure 1. Spectrograms of banded mongoose close calls
Spectrograms of close calls of the three individuals (in rows 1 to 3) associated with the three different behavioural contexts: **a.**) digging; **b.**) searching; **c.**) moving between foraging patches. The calls in the first and second row are of females, while calls in the third row are of a male. Calls of the individuals in the second and third row are from the same social pack. The solid black arrows indicate the individually stable foundation of the call, while the dashed arrows indicate the harmonic tonal segment (Hamming, FTT=1024, overlap=97.87%, frequency resolution=43h).

Table 2. Individual vocal cue classification.

Group	#[a]	Random[b]	Whole call CV-values (%)	Noisy segment CV-values (%)	Harmonic segment CV-values (%)
1B	8	12.5	48.1***	45.0***	25.0
1H	14	7	26.1*	40.0***	11.4
11	7	14	42.0***	48.0***	22.0
15	7	14	61.5***	61.1***	22.5

The percentage of correct classification after cross-validation (CV) to individuals within each of the four study groups compared to that expected by chance; Results for the whole call, noisy segment and harmonic segment are given; *p*–values are derived from bootstrapping method ; • $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

[a] Number of individuals tested

[b] Expected by chance.

Table 3. Behavioral vocal cue classification.

Part analyzed	Behavior	Individuals	ncce
Whole call	digging–searching	30	3.340•
	digging–moving	25	40.640***
	searching–moving	20	30.610***
Noisy segment	digging–searching	30	1.500
	digging–moving	25	34.850
	searching–moving	20	23.100
Harmonic segment	digging–searching	18	78.040***
	digging–moving	30	77.440***
	searching–moving	30	67.600**

The pDFA classification results for pairwise comparisons between behaviours.; Results for the whole call, noisy segment and harmonic segment are given.; The results of the pDFA is the number of correctly cross-classified elements (ncce); • $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Discussion

Banded mongoose close calls, consisting of a single syllable, were not only individually distinct, but also differed in their acoustic structure depending on the current behaviour of the signaler. This acoustic variation depended on the behavioural context encoded within a harmonic extension of the basic noisy segment of the close call. To our knowledge this is the first example of temporal segmentation

as a means of encoding multiple types of information within a call consisting of a single syllable in an animal vocalisation. Variation in spectral aspects (for example, fundamental frequency) of the more noisy call element verify previous findings of individual cues in close calls of banded mongoose (Müller and Manser 2008). In that study, Müller and Manser (2008) showed, using playback experiments that pups are able to discriminate between close calls of their escorting adult and the close calls of other adults. Their results suggest that individual vocal cues of these close calls are meaningful to receivers. Additionally, here we found group specific vocal cues. Such cues of group identity may arise because the physical characteristics that determine vocal characteristics of an individual (for example, vocal fold length (for F0) and/or vocal tract length (for formants)) are, on average, more similar among group members than non-group members. Another possibility in species with vocal flexibility and where individuals change groups is that individuals converge to match the vocal group cue of the new group after switching (Briefer and McElligott 2012; Candiotti et al. 2012). At present it is unknown which of these two processes is applicable for the banded mongoose. In contrast, temporal features (for example, duration) of the tonal harmonic segment of the call seem to encode the behavioural vocal cues. Future research using playback experiments will need to be conducted to investigate if behavioural context vocal cues are used by receivers.

While many animal signaling systems, including human speech, use concatenation of acoustically-separate syllables to enrich and extend the signaling space (for example in birdsong; Elfstörm 1990; Nelson and Poesel 2007, rock hyraxes (Koren and Geffen 2009) or cetacean species (Payne and McVay 1971; Ford 1989)), human speech also encodes information into individual syllables. By combining stop consonants with different vowels at a phonological level, syllables are created that have different meanings. Thus, a stop consonant like /b/ versus /p/ can be combined with a vowel like /a/ or /o/ to create a richer signalling unit than either class (that is, stop consonants or vowel) alone could provide. Such combinations (versus 'syntactic' concatenation of syllables and words) are a core feature of the phonological component of human spoken language (Hauser and Fitch 2003). The temporally segmented fashion in which banded mongooses encode multiple cues into a single syllable close call is analogous to this system. Moreover, our study provides an example of a discrete individual 'element' in a graded call containing information regarding individuality. The noisy, yet stable, segment of the close call, explained almost as much individual variation as the whole call. This implies that, despite the graded nature of the close call, individual identity is encoded in a discrete way.

The functional aspect of the discrete identity cue in combination with a graded behavioural cue seems analogous to human communicative contexts, when sender and receiver cannot see each other. For example, in the drum or whistle languages of tribes in the remote and isolated conditions of mountainous or densely forested areas, discrete signals are used to announce identity and other information to avoid ambiguity (Stern 1957; Meyer and Gautheron 2006). Similarly, in radio conversations in aviation between pilots and control towers, identity and additional information are shared in a highly standardized order (that is, You Me Where What With; chapter 5 Todd 2009). Signals in these 'conversations' are intentionally chosen for their clarity to the receivers (Green 1975; Ong 1977). In particular in species that are constantly moving as a cohesive unit, in their search for food or shelter, and where the identification of an individual cannot be based on its spatial position, acoustic individual identity may be a crucial aspect for the successful operation of the system. This is true for banded mongooses where coordination of foraging and movement facilitates the successful functioning of the overall social system. Temporal segregation of vocal cues may enable banded mongooses to reliably encode dual information sets regarding an individual's identity and its current behavioural context.

Our study on banded mongoose close calls demonstrates temporal segregation within a single syllable call type. However, reviewing spectrograms of other species' calls, available in the literature, reveal that our findings may not be unique to banded mongooses. For example, the well-known 'whine-chuck' advertisement call of the túngara frog (*Physalaemus pustulosus*) provides another example of segregation of information within a single syllable, where whines encode the species identity and the chucks refer to male quality (Ryan 1983a; Ryan 1983b). Such a system is highly advantageous in providing detailed reliable information in an otherwise ambiguous graded system. Human speech (Green 1975; Nelson and Marler 1990; Dooling 1992; Hauser 1996), and elements of some other species' vocal repertoires such as Barbary macaque (*Macaca sylvanus*; Fischer et al. 1995; Fischer and Hammerschmidt 2001), chimpanzee (*Pan troglodytes*; Marler and Mundinger 1975; Slocombe et al. 2009) and Japanese macaque (*Macaca fuscata*; Green 1975) are, from the production side, classified as a graded system, yet perceived by the receivers as discrete (Marler 1976; Fischer et al. 1995; Hauser 1996; Fischer and Hammerschmidt 2001; Slocombe et al. 2009). Graded signals have the potential to convey subtle and complex information, but potentially suffer from heightened ambiguity (Green 1975; Marler 1975). This ambiguity can partly be resolved by meaningful, within-category, classification of a graded signal into perceptually discrete signals (Marler 1975; Harnad 1987). It has been hypothesized that this perception of a graded continuum as a series of

discrete units was a crucial stage in the evolution of human language (Marler 1975; Marler 1976). This analogous ability in banded mongoose demonstrates that animal communication systems also have the potential to convey a rich set of information in an acoustically sophisticated way.

Recent studies have shown that some free ranging primates use meaningful call- and element-combinations to vastly increase the range of information that can be decoded by listeners (Crockford and Boesch 2005; Arnold and Zuberbühler 2006; Clarke et al. 2006; Arnold and Zuberbühler 2008; Endress et al. 2009; Ouattara et al. 2009a; Ouattara et al. 2009b; Schel et al. 2009). This may be particularly important for forest species living in dense vegetation, where no visual cues can be used to verify the information content or context of the signal (Arnold and Zuberbühler 2006; Arnold and Zuberbühler 2008). In the same way, we suggest that species that use vocal cues ultimately benefit from an increased informational repertoire and, therefore, similar species demonstrating combinatorial calling behaviour could be expected to make use of multiple vocal cues and benefit from temporal segregation of information. Vocal cues predominantly encode individual related cues of the sender (for example, identity or male quality) and we, therefore, predict temporal segregation to evolve when signallers could benefit from unambiguous multiple vocal cues. Call combinations have been hypothesized to occur in response to discrete external events (for example, alarm calls) or behavioural contexts, but not directly related to characteristics of the signaller (Arnold and Zuberbühler 2006; Ouattara et al. 2009b). Species with graded vocal systems would especially benefit from the use of unambiguous vocal cues, since these would; *i*) avoid the lack of clarity that generally occurs in graded vocalizations, and *ii*) potentially enhance the reliability of categorization by receivers of graded signals into discrete units.

Conclusion

Our results show that considerable acoustic variation underlies the close calls of banded mongooses with specific information in temporarily segregated vocal cues. Through the segregation of acoustic information, the potential trade-off in reliability between vocal cues can be avoided. Many nonhuman-animals have small vocal repertoires (Zuberbühler 2003; Arnold and Zuberbühler 2006; Arnold and Zuberbühler 2008) and call combinations are one way animals can get around the limited information content of a finite vocal repertoire. Here we demonstrate that temporarily distinct acoustic segments relating to specific vocal cues provide an equally effective and reliable solution to this problem and represent an additional dimension to the complexity underlying information coding in animal vocal com-

munication. To what extent these are used throughout the animal kingdom is an important question to be addressed in the future, as it may help us to identify the selective pressures that gave rise to these kinds of abilities in non-human animals and potentially also in humans.

Methods

Study population

The study site was located in Uganda, in the Queen Elizabeth National park (0°12S; 29°54E). The study site and the habituated population have been described in detail elsewhere (Cant 1998; Jordan et al. 2010). During the period of data collection (February 2009 to July 2011), the study population consisted of six habituated groups and three semi-habituated groups, with group sizes ranging from 6 to 50+ individuals. In five groups, most individuals were habituated to a level that allowed us to follow them with a microphone and to do detailed focal watches. As part of the Banded Mongoose Research Project long-term data collection protocol, all animals were tagged with subcutaneous transponders (TAG-P-122GL, Wyre Micro Design Ltd., UK), whereas for field identification individuals were given small hair cuts or, for less habituated fully grown adults, colour-coded plastic collar (weight ≤ 1.5 g, regularly checked to ensure a loose fit, Jordan et al. 2010).

Recording methods

All close calls used in the acoustic analysis were recorded from well-habituated adult (≥ 1 year) banded mongooses at a distance of approximately 1 to 2 m, using a Sennheiser directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40-20000 Hz ± 2.5 dB, Old Lyme, Connecticut, U.S.A.) connected to a Marantz PMD-660 solid state (Marantz Japan Inc.) or a M-Audio Microtrack II (Avid Technology USA Inc.). Calls were recorded in wav format with 16 bits and 44.1 kHz sample rate. Calls were recorded as part of detailed behavioural focal watches or during *ad libitum* sampling recording sessions. In 2009, audio recordings were made at the same time as video focal watches to record behaviour (Canon HF100); in 2010/11, commentaries on behaviour were added to the audio recording. It was noted whether the individual was a.) digging, b.) searching, or c.) moving within the foraging patch of the group (Table 1 and for details of behaviour see (Bousquet et al. 2011)). For the acoustic analysis, calls with high signal-to-noise ratio were selected, using Avisoft SASLab Pro 5.18 (R. Specht, Berlin, Germany) (Specht 2011). Only individuals for which we had at least five calls in at least two of the behavioural contexts were included in the analysis.

For individuals where more than five calls were available, we randomly selected five calls (Mundry and Sommer 2007). The calls are available in the Labarchives repository (`http://dx.doi.org/10.6070/H4W37T8Q`; *Banded mongoose close calls*).

Acoustic analysis

A 1,024-point fast Fourier transformation (Hamming window; time step: 0.07 ms; overlap: 96.87%; frequency range: 44.1 kHz; frequency resolution: 43 Hz) was conducted for all calls, using Avisoft. We manually assigned labels to the whole call, the noisy base of the call and, if present, the harmonic part of the call (Figure 1). We then used a batch processing option to obtain automatic measurements for 12 parameters (Table 4). The minimum frequency is the lowest frequency of the amplitude exceeding this threshold (-20 dB), while the maximum frequency is the highest frequency of the amplitude exceeding this threshold. The bandwidth is the difference between minimum and maximum frequency. These quartile variables characterize the distribution of energy across the spectrum and indicate the frequency below which 25, 50 or 75%, respectively, of the energy can be found. The distance between quartile 75% and quartile 25% is a measure of the pureness of the sound. The 50% quartile also indicates the mean frequency. All mean frequency measures were obtained from the mean spectrum of each call or call component, while the three quartiles were also measured from the point within the call or call component that had the maximum amplitude (Specht 2011). We also calculated the transition onset (fundamental frequency (F0) at the onset of call minus F0 at the middle of the call) and offset (F0 at the middle of the call minus F0 at the end of the call) (Townsend et al. 2010). The automatic measurements were checked by visual inspection of the graphic results of the measurements in the spectrograms.

Statistical analysis

We conducted all analyses in R, version 2.14 (R Development Core Team 2010), using the software packages 'car' (Fox and Weisberg 2011), 'kla' (Weihs et al. 2005), 'lme4' (Bates 2011), and 'MASS' (Venables and Ripley 2002). The analyses described below were done on the whole call, on the 'noisy' segment of the call, and if present, on the 'harmonic segment' of the call (Figure 1). We performed linear mixed effect models (lmer) on the acoustic variables to calculating variance inflation factors and obtaining a subset of acoustic parameters that was free from multicollinearity as this is essential for the proper functioning of the discriminant function analysis (DFA). It has been argued that conventional DFA provides grossly inflated levels of overall significance of discriminability when using multiple samples of the same individual (Mundry and Sommer 2007) and that in such cases a permuted discriminant function

Table 4. Overview of parameters used and their values per call segment (mean+(sd)).

			Whole call	
Acoustic parameters		**Digging**	**Moving**	**Searching**
Duration	(s)	0.05 ± (0.02)	0.12 ± (0.04)	0.09 ± (0.04)
Bandwidth	(mean Hz)	1,472 ± (428)	1,526 ± (378)	1,439 ± (382)
F0	(mean Hz)	263 ± (100)	467 ± (89)	380 ± (110)
Onset		20 ± (150)	-456 ± (1,752)	-205 ± (1,020)
Offset		-133 ± (814)	204 ± (1,694)	-184 ± (1,781)
Max freq.	(Hz)	1,587 ± (427)	1,675 ± (373)	1,575 ± (375)
Min. freq.	(Hz)	114 ± (31)	149 ± (55)	135 ± (43)
Peak frequency	(mean Hz)	370 ± (167)	490 ± (123)	404 ± (106)
Quartile 25%	(mean Hz)	430 ± (74)	525 ± (82)	469 ± (73)
Quartile 50%	(mean Hz)	753 ± (96)	918 ± (213)	846 ± (199)
Quartile 75%	(mean Hz)	1,426 ± (539)	2,730 ± (1,748)	2,217 ± (1,615)
Quartile 25%	(max Hz)	454 ± (77)	533 ± (77)	481 ± (78)
Quartile 50%	(max Hz)	802 ± (123)	942 ± (184)	898 ± (240)
Quartile 75%	(max Hz)	1,803 ± (1,033)	2,734 ± (1,745)	2,507 ± (1,738)
			Initial noisy segment	
		Digging	**Moving**	**Searching**
Duration	(s)	0.04 ± (0.01)	0.03 ± (0.01)	0.03 ± (0.01)
Bandwidth	(mean Hz)	1,534 ± (457)	1,542 ± (473)	1,534 ± (426)
F0	(mean Hz)	225 ± (94)	249 ± (138)	218 ± (92)
Onset		45 ± (138)	127 ± (963)	44 ± (186)
Offset		-46 ± (129)	-146 ± (951)	-79 ± (713)
Max freq.	(Hz)	1,646 ± (455)	1,654 ± (470)	1,650 ± (417)
Min. freq.	(Hz)	112 ± (26)	112 ± (28)	116 ± (30)
Peak frequency	(mean Hz)	380 ± (186)	378 ± (195)	363 ± (178)
Quartile 25%	(mean Hz)	439 ± (74)	473 ± (90)	450 ± (79)
Quartile 50%	(mean Hz)	754 ± (92)	838 ± (163)	795 ± (110)
Quartile 75%	(mean Hz)	1,329 ± (387)	2,300 ± (1,744	1,787 ± (1,250
Quartile 25%	(max Hz)	465 ± (77)	497 ± (96)	473 ± (83)
Quartile 50%	(max Hz)	797.3 ± (100)	914 ± (270)	849 ± (157)
Quartile 75%	(max Hz)	1,654 ± (865)	2,847 ± (1,997)	2,234 ± (1,612)
			Harmonic segment	
		Digging	**Moving**	**Searching**
Duration	(s)	0.03 ± (0.02)	0.08 ± (0.04)	0.06 ± (0.03)
Bandwidth	(mean Hz)	1,185 ± (405)	1,307± (394)	1,283 ± (474)
F0	(mean Hz)	350 ± (70)	472 ± (83)	410 ± (82)
Onset		-10 ± (59)	-83.0 ± (1,444)	-6 ± (789)
Offset		-177± (1,294)	-19 ± (1,134)	-176.4 ± (1,284)
Max freq.	(Hz)	1,343 ± (408)	1,572 ± (390)	1,513 ± (463)
Min. freq.	(Hz)	158 ± (83)	264 ± (93)	230 ± (97)
Peak frequency	(mean Hz)	350 ± (88)	485 ± (115)	409 ± (84)
Quartile 25%	(mean Hz)	414 ± (76)	536 ± (89)	471 ± (81)
Quartile 50%	(mean Hz)	769 ± (316)	967 ± (285)	895 ± (301)
Quartile 75%	(mean Hz)	2,346 ± (1,514)	2,861 ± (1,927)	2,784 ± (2,037)
Quartile 25%	(max Hz)	419 ± (76)	546 ± (91)	491 ± (98)
Quartile 50%	(max Hz)	802 ± (280)	976 ± (210)	940 ± (317)
Quartile 75%	(max Hz)	2,505 ± (1,598)	2,797.6 ± (1,821)	2,801 ± (1,956)

analysis (pDFA) should be used. We controlled for repeated sampling of groups and individuals by fitting 'individual' nested in 'group' as a random factor (Crawley 2007). We used an adapted form of the variance inflation factors (VIF) analysis that worked directly on predictors in lmer models (Austin Frank, pers. comm.) to detect multicollinearity in the acoustic parameters. Only parameters with a VIF ≤ 2.5 were included in the analyses. The remaining parameters were entered into a DFA to determine the correct classification probabilities of close calls to i.) behaviour while controlling for individual and ii.) individuals while controlling for behaviour. DFA identifies linear combinations of predictor variables that best characterize the differences among groups and combines the variables into one or more discriminant functions, depending on the number of groups to be classified (Venables and Ripley 2002; Weihs et al. 2005). This method of analyses provides a classification procedure that assigns each call to its appropriate class (correct assignment) or to another class (incorrect assignment). A stepwise variable selection was performed for the DFA. The initial model consisted of the parameters that remained after the selection with the linear effect model and the VIF analysis; in subsequent steps new models were generated by either including or excluding single variables in the model. This resulted in a performance measure for these models that were estimated by cross-validation, and if the maximum value of the chosen criterion was better than the previous model, the corresponding variable was included or excluded. This procedure was stopped once the new best value, after including or excluding any variable, did not exceed a 5% improvement. The number and type of variables included in the analysis differed per analysis and sub-analysis. Duration was included in all behavioural context specific tests. The number of variables included was smaller than the number of individuals included in the test (Mundry and Sommer 2007). For external validation, we used a leave-one-out cross-validation procedure and estimated the significance levels for correct statistical assignment of calls using *post hoc* 'bootstrapping' analyses. This method determined the probability that a cross-validated correct assignment value was achieved by chance (Müller and Manser 2008). Our data for behavioural, group, and sex vocal cues were two factorial (test factor and individual) and contained five call examples per individual, we, therefore, used a crossed pDFA (Mundry, pers. comm.). Furthermore, to ensure no differences resulted from variation in sex or group, we also performed pDFAs while keeping these two additional variables constant. We performed four pDFAs to test for overall and the pairwise comparison between behavioural contexts. In addition, we performed two additional pDFAs to test for the group cue and sex cues (both while controlling for individual). From one of the groups, we did not have calls from a large enough number of individuals

to perform a classification analysis, and, therefore, the group vocal cue analysis was conducted on four groups only.

Ethical note

This research was carried out under license from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority. Trapping and marking procedures, which are part of the long-term research program, followed the guidelines of the Association for the Study of Animal Behavior (Cant 2000; Jordan et al. 2010).

Abbreviations

DFA, discriminant function analysis; F0, fundamental frequency; lmer, linear mixed effect models; ncce, number of correctly cross-classified elements; pDFA, permutated discriminant function analysis; VIF, variance inflation factors.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

DJ designed the study, collected data in the field, analyzed the data and wrote up of the paper. MC helped to write the paper and provided logistical support in the field. MM designed research and helped to write the paper. All authors read and approved the final manuscript.

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References

Arnold, K and K Zuberbühler (2006). "Language evolution: Semantic combinations in primate calls". *Nature*, 441(7091), 303.

— (2008). "Meaningful call combinations in a non-human primate". *Current Biology*, 18(5), R202–R203.

Bates, DM (2011). *lme4: Mixed-effects modeling with R*. New York: Springer.

Boughman, JW and GS Wilkinson (1998). "Greater spear-nosed bats discriminate group mates by vocalizations". *Animal Behaviour*, 55(6), 1717–1732.

Bousquet, CAH, DJT Sumpter, and MB Manser (2011). "Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 278(1711), 1482–1488.

Bradbury, JW and SL Vehrencamp (1998). *Principles of animal communication*. New York: Sinauer Associates.

Briefer, E and AG McElligott (2012). "Social effects on vocal ontogeny in an ungulate, the goat (*Capra hircus*)". *Animal Behaviour*, 83(4), 991–1000.

Briefer, E, E Vannoni, and AG McElligott (2010). "Quality prevails over identity in the sexually selected vocalisations of an ageing mammal". *BMC Biology*, 8(35), 1–15.

Briefer, E et al. (2008). "How to identify dear enemies: the group signature in the complex song of the skylark *Alauda arvensis*". *Journal of Experimental Biology*, 211(3), 317–326.

Candiotti, A, K Zuberbühler, and A Lemasson (2012). "Convergence and divergence in Diana monkey vocalizations." *Biology Letters*, 8(3), 382–385.

Cant, MA (1998). "Communal breeding in banded mongooses and the theory of reproductive skew". PhD thesis. Cambridge, UK: University of Cambridge.

— (2000). "Social control of reproduction in banded mongooses". *Animal Behaviour*, 59(1), 147–158.

Charlton, BD, Z Zhang, and RJ Snyder (2009). "Vocal cues to identity and relatedness in giant pandas (*Ailuropoda melanoleuca*)". *Journal of the Acoustical Society of America*, 126(5), 2721–2732.

Charlton, BD et al. (2010). "Female giant panda (*Ailuropoda melanoleuca*) chirps advertise the caller's fertile phase". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 277(1684), 1101–1106.

Clarke, E, UH Reichard, and K Zuberbühler (2006). "The syntax and meaning of wild gibbon songs". *PLoS ONE*, 1(1), e73.

Clutton-Brock, TH and SD Albon (1979). "The roaring of red deer and the evolution of honest advertising". *Behaviour*, 69, 145–170.

Crawley, MJ (2007). *The R book*. Chichester: John Wiley & Sons.

Crockford, C and C Boesch (2005). "Call combinations in wild chimpanzees". *Behaviour*, 142, 397–421.

Crockford, C et al. (2004). "Wild chimpanzees produce group-specific calls: a case for vocal learning?" *Ethology*, 110(3), 221–243.

DaCunha, RGT and RW Byrne (2008). "The use of vocal communication in keeping the spatial cohesion of groups: intentionality and specific functions". In: *South American primates: comparative perspectives in the study of behavior, ecology, and conservation*. Ed. by PA Garber et al. New York: Springer, pp. 341–363.

Dooling, RJ (1992). "Hearing in birds". In: *The Evolutionary Biology of Hearing*. Ed. by DB Webster, RR Fay, and AN Popper. Berlin Heidelberg: Springer, pp. 545–560.

Elfstörm, ST (1990). "Responses of territorial meadow pipits to strange and familiar song phrases in playback experiments". *Animal Behaviour*, 40(4), 786–788.

Endress, AD et al. (2009). "Evidence of an evolutionary precursor to human language affixation in a non-human primate". *Biology Letters*, 5(6), 749–751.

Fischer, J and K Hammerschmidt (2001). "Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls." *Animal Cognition*, 4(1), 29–35.

Fischer, J, K Hammerschmidt, and D Todt (1995). "Factors affecting acoustic variation in Barbary macaque (*Macaca sylvanus*) disturbance calls". *Ethology*, 101(1), 51–66.

Fischer, J et al. (2004). "Baboon loud calls advertise male quality: acoustic features and relation to rank, age, and exhaustion." *Behavioral Ecology and Sociobiology*, 56(2), 140–148.

Fitch, WT (1997). "Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques". *Journal of Acoustical Society of America*, 102, 1213–1222.

— (2000). "Skull dimensions in relation to body size in nonhuman primates: the causal bases for acoustic allometry." *Zoology*, 103(1-2), 40–58.

Ford, JKB (1989). "Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia". *Canadian journal of Zoology*, 67(3), 727–745.

Fox, J and S Weisberg (2011). *An R Companion to Applied Regression*. 2nd. Los Angeles, CA: Sage Publications.

Furrer, RD (2009). "Leadership and group-decision-making in banded mongooses (*Mungos mungo*)". PhD thesis. Zurich, Switzerland: University of Zurich.

Green, S (1975). "Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study". *Primate Behavior, Developments in Field and Laboratory Research*, 2, 1–102.

Hammerschmidt, K and J Fischer (2008). "Constraints in primate vocal production". In: *The evolution of communicative creativity: From fixed signals to contextual flexibility*. Ed. by U Griebel and K Oller. Cambridge, MA: The MIT Press, pp. 93–119.

Harcourt, AH, KJ Stewart, and MD Hauser (1993). "Functions of wild gorilla 'close' calls. 1. repertoire, context, and interspecific comparison". *Behaviour*, 124, 89–112.

Harnad, S (1987). *Categorical perception : the groundwork of cognition*. Cambridge, UK: Cambridge University Press.

Hauser, MD (1996). *The evolution of communication*. Cambridge, MA: MIT Press.

Hauser, MD and WT Fitch (2003). "Language Evolution: The States of the Art". In: *Language Evolution: The States of the Art*. Ed. by M Christiansen and S Kirby. Oxford: Oxford University Press. Chap. What Are the Uniquely Human Components of the Language Faculty?, pp. 317–337.

Jameson, JW and JF Hare (2009). "Group-specific signatures in the echolocation calls of female little brown bats (*Myotis lucifugus*) are not an artefact of clutter at the roost entrance". *Acta Chiropterologica*, 11, 163–172.

Janik, VM, G Dehnhardt, and D Todt (1994). "Signature whistle variation in a bottlenosed dolphin, *Tursiops truncatus*". *Behavioral Ecology and Sociobiology*, 35(4), 243–248.

Jansen, DAWAM, MB Cant, and MB Manser. *Banded mongoose close calls*. LabArchives, `http://dx.doi.org/10.6070/H4W37T8Q`.

Jordan, NR et al. (2010). "Scent marking within and between groups of wild banded mongooses". *Journal of Zoology*, 280(1), 72–83.

Kondo, N and S Watanabe (2009). "Contact calls: Information and social function". *Japanese Psychological Research*, 51(3), 197–208.

Koren, L and E Geffen (2009). "Complex call in male rock hyrax: a multi-information distributing channel." *Behavioral Ecology and Sociobiology*, 63(4), 581–590.

Marler, P (1975). "On the origin of speech from animal sounds." In: *The role of speech in language*. Ed. by J Kavanagh and J Cutting. Cambridge, MA: MIT Press. Chap. On the origin of speech from animal sound, pp. 11–37.

— (1976). "Social organization, communication and graded signals the chimpanzee and the gorilla". In: *Growing points in ethology*. Ed. by PPG Bateson and RA Hinde. Cambridge: Cambridge University Press, pp. 239–281.

Marler, P and PC Mundinger (1975). "Vocalizations, social-organization and breeding biology of twite *Acanthus flavirostris*". *Ibis*, 117, 1–6.

Marler, P (1960). "Bird song and mate selection". In: *Animal sounds and communication*. Ed. by W Lanyon and W Tavalga. Port Jervis, NY: Lubrecht & Cramer, pp. 348–367.

Mathevon, N et al. (2010). "What the hyena's laugh tells: Sex, age, dominance and individual signature in the giggling call of *Crocuta crocuta*". *BMC Ecology*, 10(1), 9.

Maynard-Smith, J and D Harper (2003). *Animal Signals*. New York: Oxford University Press.

Messeri, P et al. (1987). "A study of the vocal repetoire of the banded mongoose (*Mungos mungo*)". *Italian journal of Zoology*, 19(22), 341–73.

Meyer, J and B Gautheron (2006). "Whistled speech and whistled languages." In: *Encyclopedia of Language and Linguistics*. Ed. by K Brown. Vol. 13. Elsevier, pp. 573–576.

Müller, CA and MB Manser (2008). "Mutual recognition of pups and providers in the cooperatively breeding banded mongoose". *Animal Behaviour*, 75(5), 1683–1692.

Mundry, R and C Sommer (2007). "Discriminant function analysis with nonindependent data: consequences and an alternative". *Animal Behaviour*, 74(4), 965–976.

Nelson, DA and P Marler (1990). "Categorical perception of natural stimulus continuum: birdsong". *Science*, 244(4907), 976–979.

Nelson, DA and A Poesel (2007). "Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song". *Animal Behaviour*, 74(4), 1073–1084.

Ong, WJ (1977). "African talking drums and oral noetics". *New Literary History*, 8(3), 411–429.

Ouattara, K, A Lemasson, and K Zuberbühler (2009b). "Campbell's monkeys concatenate vocalizations into context-specific call sequences". *Proceedings of the National Academy of Sciences of the United States of America*, 106(51), 22026–22031.

— (2009a). "Anti-predator strategies of free-ranging Campbell's monkeys". *Behaviour*, 146, 1687–1708.

Owren, MJ, RM Seyfarth, and DL Cheney (1997). "The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): Implications for production processes and functions". *Journal of the Acoustical Society of America*, 101(1), 2951–2963.

Payne, RS and S McVay (1971). "Songs of humpback whales". *Science*, 173(3991), 57–64.

Reby, D and K McComb (2003). "Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags". *Animal Behaviour*, 65(3), 519–530.

Reby, D et al. (1998). "Individuality in the groans of fallow deer (*Dama dama*) bucks". *Journal of Zoology*, 245(1), 79–84.

Rendall, D (2003). "Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons." *Journal of the Acoustical Society of America*, 113(6), 3390–3402.

Rendall, D et al. (1999). "The meaning and function of grunt variants in baboons". *Animal Behaviour*, 57(3), 583–592.

Riede, T and WT Fitch (1999). "Vocal tract length and acoustics of vocalization in the domestic dog *Canis familiaris*". *Journal of Experimental Biology*, 202, 2859–2867.

Rood, JP (1975). "Population dynamics and food habits of the banded mongoose". *East Africa Wildlife journal*, 13, 89–111.

Ryan, MJ (1983b). "Sexual selection and communication in a Neotropical frog, *Physalaemus pustulosus*". *Evolution*, 39(2), 261–272.

— (1983a). "Frequency modulated calls and species recognition in a Neotropical frog." *Journal of Comparative Physiology*, 150(2), 217–221.

Schel, AM, S Tranquilli, and K Zuberbühler (2009). "The alarm call system of two species of black-and-white colobus monkeys (*Colobus polykomos* and *Colobus guereza*)". *Journal of Comparative Psychology*, 123(2), 136–150.

Shapiro, AD (2010). "Recognition of individuals withing social group: signature vocalizations". In: *Handbook of mammalian vocalization*. Ed. by SM Brudzynski. Oxford: Elsevier Academic Press, pp. 495–503.

Slocombe, KE, SW Townsend, and K Zuberbühler (2009). "Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: Evidence from a playback study". *Animal Cognition*, 12(3), 441–449.

Specht, R (2011). *Avisoft SASLab Pro. User's Guide for version 5.1*. Avisoft Bioacoustics. Berlin.

Stern, T (1957). "Drum and whistle 'languages': an analysis of speech surrogates". *American Anthropologist*, 59(3), 487–506.

Todd, SC (2009). *The pilot's handbook*. Beverly, MA: Pilot Handbook Publishing.

Townsend, SW, C Allen, and MB Manser (2012). "A simple test of vocal individual recognition in wild meerkats". *Biology Letters*, 8(2), 179–182.

Townsend, SW, LI Hollen, and MB Manser (2010). "Meerkat close calls encode group-specific signatures, but receivers fail to discriminate". *Animal Behaviour*, 80(1), 133–138.

Townsend, SW, M Zoettl, and MB Manser (2011). "All clear? Meerkats attend to contextual information in close calls to coordinate vigilance". *Behavioral Ecology and Sociobiology*, 65(10), 1927–1934.

Vannoni, E and AG McElligott (2008). "Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males". *PLoS ONE*, 39, e3113.

Venables, WN and BD Ripley (2002). *Modern Applied Statistics with S*. 4th. Berlin Heidelberg: Springer.

Weihs, C et al. (2005). "klaR Analyzing German Business Cycles". In: *Data analysis and decision support*. Ed. by D Baier, R Decker, and L Schmidt-Thieme. Berlin: Springer, pp. 335–343.

Zuberbühler, K (2003). "Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language". *Advances in the Study of Behavior*, 33, 265–307.

3

Context-specific call sequences in the banded mongoose

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Context-specific call sequences in the banded mongoose

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Abstract

Animal may potentially overcome their anatomical constraints in the production of new call types by combining existing calls in their repertoire into non-random sequences. While there is a growing body of evidence for such concatenation of calls in the context of predation, in the affiliative context evidence is limited. In this study we investigated the possible combinatorial properties of the most frequently emitted call type in the banded mongoose (*Mungos mungo*), the close call. The data were collected on a wild, but habituated, population in Uganda. Banded mongoose close calls contain temporally separated cues indicating individuality and behaviour. We found that banded mongooses use these close calls in combination with other call elements. These sequences resulted in new call types, namely the 'excitement'-, 'lead-', and 'lost-' call. The individually distinct segment of the close call remained unchanged in these sequences. The additional elements related to the specific behavioural contexts did not only differ in their acoustic structure, but also varied in the number of elements emitted after the preceding close call. These results show that banded mongoose also use non-random concatenation of calls into more complex sequences, likely increasing the potential information to receivers. Furthermore, this study shows that non-random concatenation of calls in the context of affiliation is also present in non-primates.

Keywords: affiliative calls, communicative complexity, call combinations, vocal signature, close call, banded mongoose

Introduction

The convention in vocal repertoire studies is to refer to repertoire size as the number of discrete calls types that a non-human animal species (hereafter, animals) produces (Blumstein and Armitage 1997; McComb and Semple 2005; Gustison et al. 2012). All species are, however, anatomically constrained in the number of different call types they can produce (Fitch 2000) and thus in the size of their vocal repertoire (i.e. counted as the number of discrete call types Fitch 2000; Zuberbühler 2003; Arnold and Zuberbühler 2008). It has been hypothesised that the evolution of meaningful call combinations have been triggered by this constraint of a limited vocal repertoire (Arnold and Zuberbühler 2006; Arnold and Zuberbühler 2008). By using existing calls in combinations animals are able to convey additional meaningful information within their existing vocal repertoire (Crockford and Boesch 2005; Arnold and Zuberbühler 2006; Clarke et al. 2006; Arnold and Zuberbühler 2008; Endress et al. 2009; Ouattara et al. 2009a; Ouattara et al. 2009b; Schel et al. 2009; Candiotti et al. 2012). Therefore, call combinations should be considered when investigating vocal repertoire sizes.

The majority of call combination studies have been conducted in the context of predation or large distance communication (i.e. the combinations of alarm calls in adult male putty-nosed monkeys, *Cercopithecus nictitans martini*, Arnold and Zuberbühler 2006; Lemasson and Hausberger 2011; Candiotti et al. 2012). A largely untouched question is whether close-range social or affiliative calls are used in meaningful sequential structures similar to the ones observed in context of predation. There is evidence that meaningful subtypes within graded call types exist in close-range social or affiliative calls (e.g baboons grunts, *Papio spp.*, Rendall et al. 1999; Fischer and Hammerschmidt 2002; chimpanzees aggression screams, *Pan troglodytes*, Slocombe and Zuberbühler 2007 and Japanese macaque 'coo' calls, *Macaca fuscata*, Green 1975). Evidence for meaningful sequential structures in a social or affiliative context is limited to recent studies on call combinations in few contexts in chimpanzees (Crockford and Boesch 2005), food calls in bonobos (*Pan paniscus*, Clay and Zuberbühler 2011) and affiliative calls in Diana monkeys (*Cercopithecus diana*, Candiotti et al. 2012).

The most common vocalization produced by many group-living mammalian and bird species is the 'contact' call. Contact calls have been shown to contain information on factors such as individual identity (Rendall 2003; Shapiro 2010), group membership (Boughman and Wilkinson 1998; Jameson and Hare 2009; Townsend et al. 2010), vigilance behaviour (Radford and Ridley 2007; Townsend et al. 2010) or current behaviour (Owren et al. 1997; Jansen et al. 2012). Contact calls therefore

have the potential to provide constant information about the producer's individual characteristics and are likely used to monitor changes in behaviour, relative spatial positioning of members in social groups and social affiliations (Harcourt et al. 1996; Rendall and Owren 2002; DaCunha and Byrne 2008; Kondo and Watanabe 2009; Townsend et al. 2011; Townsend et al. 2012; Reber et al. in review). In species where contact calls predominantly play an important role in short-distance communication, contact calls are better described as close calls (Harcourt et al. 1993; Townsend et al. 2010).

Here we investigated the possible combinatorial properties of the most frequently emitted contact call in the banded mongoose (*Mungos mungo*). Banded mongooses are a small ($\leq$ 2 kg) communally breeding mongoose species, which are commonly found in the savannah and open forests of central and eastern Africa. Members of a banded mongoose pack forage as a cohesive unit and cooperate in pup care (Rood 1974; Gilchrist 2004), predator avoidance (Müller and Manser 2008; Furrer 2009) and territory defence (Rood 1983; Cant 1998). Banded mongooses have an extensive graded vocal repertoire (Messeri et al. 1987; Jansen 2013). Individuals use vocalisations in a variety of behavioural and social contexts, such as group movement (Furrer 2009; Fairbanks et al. 2011), predator avoidance (Jansen 2013), aggressive encounters among group members or between groups (Müller and Manser 2007; Furrer et al. 2011), group recruitment (Furrer and Manser 2009; Furrer et al. 2011), pup begging (Bell 2007; Metherell 2009), as well as during dominance interactions (Jansen 2013). The banded mongoose close calls contain temporally separated cues for individuality and behaviour (Jansen et al. 2012). The individual identity of the caller is conveyed in the initial stable part (solid arrow in Figure 1), while the current behaviour is indicated by the harmonic extension (dashed arrow in Figure 1). Preliminary field observations suggested that the close calls were also used in combinations with various additional elements resulting in new call types in three different behavioural contexts, namely when individuals got excited about wet ground or the onset of rain (Messeri et al. 1987), attempted to or were leading the group (Furrer 2009), and when an individual seemed to have lost contact with the group (Table 1 and Figure 2). Here we investigate how banded mongooses combine calls in their graded vocal repertoire. We then discuss how banded mongooses increase variation in the meaning of their vocal repertoire, despite being limited in their number of discrete call types.

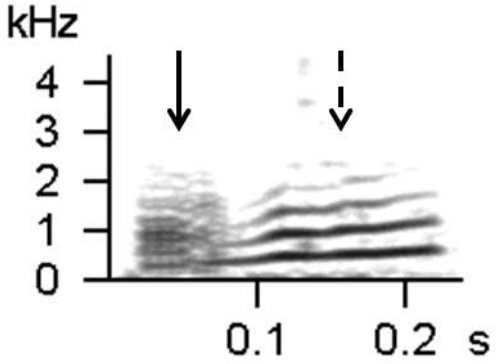

Figure 1. Spectrogram of a typical 'moving' close call. The solid black arrow indicates the individually stable segment of the call, while the dashed arrow indicates the harmonic tonal segment.

Table 1. Overview of different call types related to behavioural contexts.

Call type	Context
Close call	Frequently used contact call, potentially to maintain social organization during foraging (see Jansen et al. 2012, for details)
Excitement call	Emitted when encountering wet ground or at onset of rain. The calls lead to recruitment of group members, but the exact function of the call is presently unknown (previously also referred to as 'Water call'; Messeri et al. 1987).
Lead call	Initiation and coordination of group movement (previously referred to as 'Moving call'; Furrer 2009).
Lost call	Emitted by individuals that got separated from their group

Methods

Study population

The study site is located in Uganda, in the Queen Elizabeth National park (0°12S; 29°054E). The study site and the wild, but habituated, population are described in detail in Cant (1998) and Jordan et al. (2010). During the three periods of data collection between Feb. 2009 and Aug. 2011, the study population consisted of four to six habituated groups and three semi-habituated groups, with group sizes ranging from 6 to 50+ individuals. Animals were classified as adults ($\geq$ 12 months), sub-adults (6–12 months), and pups ($\leqq$ 3 months, Cant 1998). As part of the Banded Mongoose Research Project long term data collection protocol, all animals were tagged with subcutaneous transponders (TAG-P-122GL, Wyre Micro Design Ltd,

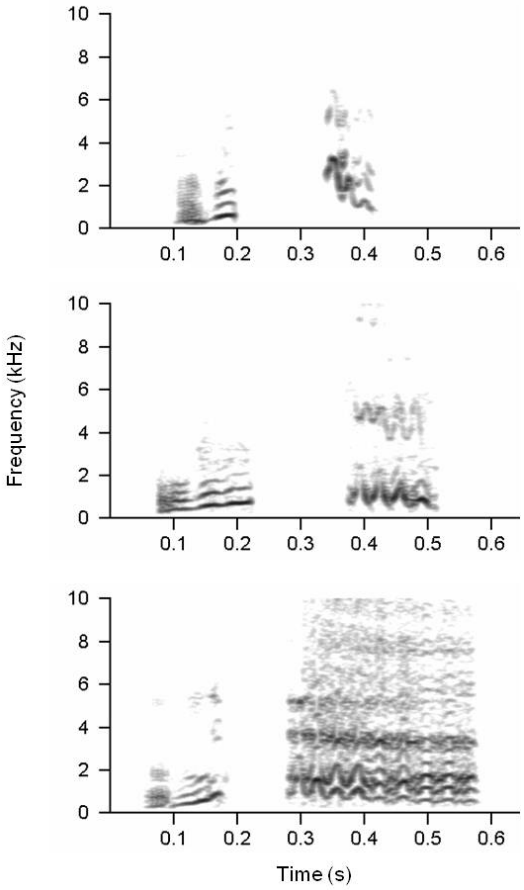

Figure 2. Typical examples of a.) excitement; b.) lead; and c.) lost calls (Gauss, FTT=1024, overlap=97.87%, frequency resolution=43 Hz).

UK), whereas for field identification, individuals were given small hair cuts or, for less habituated fully grown adults, colour-coded plastic collars (weight 1.5 g, regularly checked to ensure a loose fit, for details see Jordan et al. 2010).

Recording methods

Vocalisations were recorded from banded mongooses at a distance of approximately 1-2m, using a Sennheiser directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40-20.000 Hz ± 2.5 dB, Old Lyme, Connecticut, U.S.A.) connected to a Marantz PMD-660 solid state (Marantz Japan Inc.), or a M-Audio Microtrack II (Avid Technology USA Inc). Calls were recorded in wav format with 16 bits and 44.1 kHz sample rate as part of detailed behavioural focal watches or during *Ad Libitum* sampling (Altman 1974) recording sessions. The individual and behavioural context were described in relation to the recorded calls.

Acoustic analysis

Calls for analysis were selected based on a good sound-to-noise ratio using Cool Edit 2000 (Syntrillium Software Corp., Phoenix, USA) and analysed in Avisoft SASLab Pro 5.18 (Specht 2012). We used calls from 31 different individuals belonging to 6 groups. To generate spectrograms of calls we carried out a $1,024 - point$ fast Fourier transformation (Gauss window, overlap: 93.75%, time resolution 1.45 ms, frequency resolution: 43 Hz). We used a batch processing option to obtain automatic measurements for 12 accoustic parameters of the various parts of the calls (Table 4). For calls that had multiple elements following the close call we took aucostic measurements on the first element that followed the close call. The automatic measurements were checked by visual inspection of the graphical results of the measurements in the spectrograms. Including many acoustic parameters enables an analysis of complex patterns without *a priori* assumptions of the importance of specific parameters (Schrader and Hammerschmidt 1997).

Analyses included parameters describing temporal and frequency dynamics and entropy of calls. For frequency- and entropy-related parameters we chose the maximum or mean of the spectrum of the entire element and the centre of the element as temporal locations of the measurements. The minimum frequency is the lowest frequency of the amplitude exceeding this threshold (-20 dB), whilst the maximum frequency is the highest frequency of the amplitude exceeding the same threshold. The bandwidth is the difference between minimum and maximum frequency. The quartile variables characterize the distribution of energy across the spectrum and indicate the frequency below which 25, 50 or 75% respectively of the energy can be found. The distance between quartile 75% and quartile 25% is a measure of the pureness of the sound. The 50% quartile also indicated the mean frequency. All mean frequency measures were obtained from the mean spectrum of each call or call component, while the 3 quartiles were also measured from the point within the call or call component that had the maximum amplitude. The fundamental frequency is defined as the lowest frequency of a periodic waveform and it is the pitch of the sound. The number of peaks indicated the number of peaks (harmonics) that exceed the threshold of -20 dB. The peak–to–peak amplitude determines the broad-band peak-to-peak amplitude and is related to the peak frequency of the FFT spectrum (Specht 2012). Lastly, for these elements, we used peak frequency values that were measured every 10 ms from the start to the end of the call to get an approximation of the temporal variation in the calls. The number of measured values depended on the duration of the call (n = total duration of the call $(ms)/10 + 1$). We used these values to calculate the maximum (max frequency

step) and average (mean frequency step) frequency differences between steps of 10 ms (Charrier et al. 2010).

Temporal sequence of close calls and additional elements

To characterise the temporal order of the different call elements in the call sequences related to the three behavioural context, we analysed the number of additional elements which followed a close call, before a close call was emitted again. We also noted if the sequence had different orders or if the elements were emitted by themselves. We did this for a set of randomly selected files recorded in the three behavioural contexts. We recorded the order of the first 10 sequences that were of good enough quality to recognise the different call elements. For the three behavioural contexts, excitement. leading and being lost we analysed respectively, 26, 28, and 19 files. This gave data on 145, 200 and 175 sequences, respectively in the according behavioural context.

Statistical analysis

All statistical analyses were conducted in R, version 2.15.2 (R Core Team 2012), using the software packages 'HH' (Heiberger 2012), 'klaR' (Weihs et al. 2005), 'lme4' (Bates 2011), and 'MASS' (Venables and Ripley 2002). The discriminant function analysis (DFA) method identifies linear combinations of predictor variables that best characterize the differences among call types and combines the selected acoustic variables into one or more discriminant functions, depending on the number of groups to be classified (Venables and Ripley 2002; Weihs et al. 2005). It provides a classification procedure that assigns each call to its appropriate class (correct assignment) or to another class (incorrect assignment). It has been argued that conventional DFA provides grossly inflated levels of overall significance of discriminability when using multiple samples of the same individual (Mundry and Sommer 2007). Therefore the acoustic parameters (hereafter parameters) of only one randomly chosen call per behavioural context per individual were entered into the DFA. This resulted in a selection of 63 vocalisations (Close call= 27, Excitement = 11, Lead = 31, Lost = 25). Prior to the analyses we rescaled the parameters for comparability. Standardized Z scores were calculated for all values. We excluded any cases in which at least one parameter had a Z score greater than 3.29. This resulted variable numbers of calls that entered the various analysis. We used Variation Inflation Factors (VIF) of the parameters to control for collinearity as this is essential for the proper functioning of DFA. VIF is a simple diagnostic method to detect evidence of collinearity between parameters. As only predictory parameters are involved with collinearity, the calculation of VIF is a function of the predictors X's but not of the response Y. The VIF for a parameter i is

$1/(1-R_i^2)$, where R_i^2 is the R^2 from a regression of predictor i against the remaining predictors. If R_i^2 is close to 1, this means that predictor i is well explained by a linear function of the remaining predictors, and, therefore, the presence of predictor i in the model is redundant. Only parameters with VIF values below 5 were included in the model as higher values are considered evidence of collinearity (Heiberger and Holland 2004; Heiberger 2012). The remaining parameters were entered to a stepwise forward parameter selection. The initial model was defined by starting with the parameter which separates the call types the best. The model was then extended by including further parameters depending on the criteria that the additional parameter *i.*) minimized the Wilks λ and *ii.*) its associated p-value still showed a statistical significance. The selected parameters were subsequently entered to a DFA. For external validation, we used a leave-one-out cross-validation procedure and estimated the significance levels for correct statistical assignment of calls using post hoc 'bootstrapping' analyses. This method determined the probability that a cross-validated correct assignment value was achieved by chance (Müller and Manser 2008). Using a similar approach we additionally analysed the close calls used in the call combinations.

Ethical note

This research was carried out under license from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority. Trapping and marking procedures, which are part of the long term research programme, followed the guidelines of the Association for the Study of Animal Behaviour (Cant 2000; Jordan et al. 2010 for details see ASAB 2006).

Results

Close call part

In the three behavioural distinct contexts related to leading the group, being lost from the group, and excitement due to wet ground or rain (Table 1), close calls typically emitted in the foraging context, were produced in combinations with additional different elements. The close calls used in these behavioural contexts showed some differences with the close call observed during foraging. The discriminate function analysis (DFA) gave an overall cross-validated correct assignment (CV) of 61.41% (Wilks $\lambda = 0.396$, $N_{21,11,28,15}$, $F_5 = 6.292$, $p < 0.001$, Table 2). This was significantly higher than expected by change (24.99%, $p = 0.002$). The variation was caused by significant differences in the harmonic extension of the call (CV = 66.67%, Wilks $\lambda = 0.336$, $N_{34,12,29,15}$, $F_5 = 7.33$, $p < 0.001$), which was significantly higher that expected by change (28.37%, $p = 0.001$). The stable noisy element did not differ between the

behavioural contexts (CV = 39.24%, Wilks $\lambda = 0.583$, $N_{27,9,29,14}$, $F_4 = 3.6$, $p = 0.05$), and was not significantly different than expected by chance (26.86%, $p = 0.180$).

Additional element related to behavioural context

The additional elements of the call types emitted in the three different contexts of leading. lost and excitement were acoustically distinct. The DFA produced a CV of 67.2% (Wilks $\lambda = 0.329$, $N_{11,27,23}$, $F_5 = 8.3$, $p < 0.001$; Table 2 & Figure 3), which was significantly higher than expected by chance (37.06%, $p = 0.014$). The first discriminant function explained 74.3% of the variance. The calls were predominately used in the appropriate behavioural contexts, although some variation was observed (Table 3). Pairwise comparisons showed that all three call types were significantly different from each other (Pairwise DFA Excitement–Lead: CV= 90.5%, $\lambda = 0.382$, $N_{11,31}$, $F_6 = 9.44$, $p = 0.008$; Excitement–Lost: 88.24%, $\lambda = 0.291$, $N_{11,23}$, $F_6 = 10.99$, $p = 0.008$; Lead–Lost: 87.23%, $\lambda = 0.379$, $N_{25,21}$, $F_5 = 13.14$, $p = 0.003$). These CV values were all significantly higher than expected by chance (Excitement–Lead: random = 61.33%, $p = 0.014$; Excitement–Lost: 57.6%, $p = 0.030$; Lead–Lost: 50.5%, $p = 0.048$). Call types differed in both temporal and frequency aspects. Frequencies varied in distribution as well as in degree of modulations (Table 4).

Table 2. Overview of classification results for the different call types.

Call types	Predicted membership			Total
	1	2	3	
1	72.7	27.3	0	100
2	3.7	81.5	14.8	100
3	8.7	21.7	69.6	100

Call types 1: Excitement; 2. Lead; 3: Lost

Table 3. Overview of behavioural contexts in which the different call types were emitted.

	Observed context					
Call types	Excitement	Leading	Lost	Foraging	Other	Total
Close call	-	-	-	21	-	21
Excitement	9	1	-	-	1	11
Lead	-	26	1	4	-	31
Lost	-	3	17	2	3	25

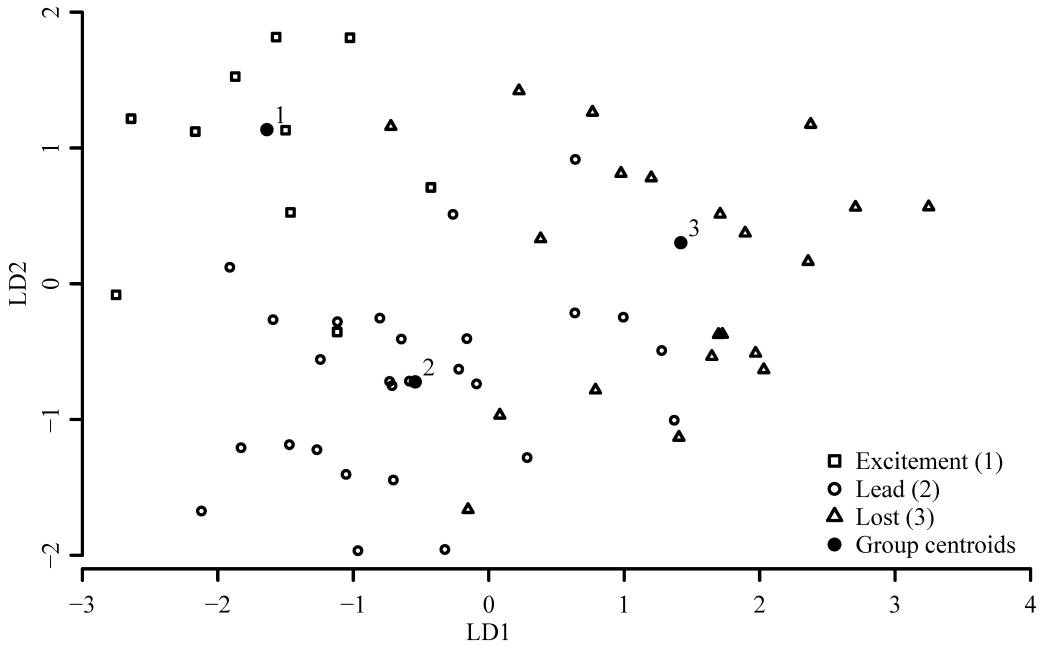

Figure 3. Discriminant function analysis scores and group centroids of call types emitted by banded mongooses in the context of excitement, leading (group movement) and being lost.

Table 4. Acoustic parameters used in the analysis.

Acoustical parameter	Location	Parameter category	Unit	Analysis
Duration	-	Temporal	s	a, b, 1,2,4
Fundamental frequency	mean	Frequency	Hz	a,b
Fundamental frequency	centre	Frequency	Hz	a,b,3
Maximum frequency	Max	Frequency	Hz	a,b
Minimal frequency	Centre	Frequency	Hz	1,2,3,4
Frequency bandwidth	Centre	Frequency distribution	Hz	4
Frequency bandwidth	Mean	Frequency distribution	Hz	1,2,3
Max. freq. of quartile 50	Centre	Frequency distribution	Hz	b, 1,4
Max. freq. of quartile 75	Centre	Frequency distribution	Hz	1
Number of peaks	Centre	Frequency modulation	-	1,2
Mean frequency step	Mean	Frequency modulation	Hz	1,2,3
Maximum frequency step	Mean	Frequency modulation	Hz	2,3
Peak-to-peak amplitude	-	Waveform	V	1,2,3,4

The acoustic parameters shown were used in discriminant function analyses of call types. Numbers in analysis column indicate with parameters where used in specific DFA: a. Overall close call, b. Harmonic extension of close call, 1. Overall call types, 2. Excitement–Lead, 3. Excitement–Lost, 4. Lead–Lost All parameters with a VIF of 5 were excluded from the parameter set. Acoustical parameters were measured at the centre of the 1^{st} element following the close call (centre) or over the duration of the whole 1^{st} element following the close call (mean).

Segment order in call sequences

The call sequences in the different behavioural contexts showed a variation in the temporal order of the close call part with the additional element. The elements were found in immediate combination with a close call in the context of excitement (92.4%; 134 out of 145 sequences), leading (97.5%; 195/200) and being lost (85.1%, 149/175). The number of additional elements related to the context between two close calls varied within context and also between context: excitement: (median ($\tilde{x}$) = 1, $q_{25} - q_{75}$ = 1 - 2, max= 18, N = 145), lead ($\tilde{x}$ = 1, $q_{25} - q_{75}$ = 1 - 1, max = 2, N = 200) and lost ($\tilde{x}$ = 2, $q_{25} - q_{75}$ = 1 - 3, max = 12, N = 175).

Discussion

In a previous study we showed that close calls of the banded mongoose contain temporally separated individual and behavioural vocal cues (Jansen et al. 2012). The individual cue formed a stable 'segment' in a graded call type and the behavioural information was conveyed in the graded harmonic segment of the call. Here we show that banded mongooses used these close calls in combination with other call elements potentially resulting in new call types, namely the 'excitement'-, 'lead-', and 'lost-' calls. In these call sequences the stable initial and individual distinct segment of the close call remained unchanged whilst the harmonic segment varied. The additional elements related to the specific behavioural context not only differed in their acoustic structure, but there was also a large variation in the number of these elements emitted after the preceding close call.

The existence of these call series directly questions what the function is of the different call elements in the different contexts. Why is the close call emitted intermittently between the other additional context specific element of being excited, lost or trying to lead the group? The elements of the excitement and lead calls were occasionally used separately (i.e. without proceeding close call) or in different order such as 'element - close call' or 'close call - element - element'. Analyses of the segmental order in these sequences showed that the lead calls were the most stereotypic of the three call types. The highest variation was observed in the contexts of being lost, although the most extreme (i.e. highest number of elements following a close call) was observed in the excitement contexts. At present we are not able establish if this variation has an influence on the 'meaning' of the call sequence. In the contexts of excitement, calls were often emitted by multiple group members simultaneously and this lead to high excitement in the group. During these recruitment events element rate was higher. For the lost calls more variation was observed and in most cases close calls were followed by two or more elements.

In cases where the individual was really lost and likely more aroused the close call was generally absent (pers. obs. DJ). This indicates that the more one of the specific contexts is pronounced, the more the associated elements are being produced, while the close calls are not emitted so frequently.

Since close calls of banded mongooses contained both individual and behavioural cues (Jansen et al. 2012), it seems unlikely that, in call sequences, the call unit functions as a meaningless call element. Instead, it seems more plausible that the information of the individual cue is mainly contained in the close call part within the call sequence. The close call could therefore function as an individual identifier combined with information on the contextual situation. In the context of foraging this contextual information is conveyed in the harmonic extension, whilst in the other three contexts it is expressed through the addition of the extra element. Similar observations exist from Diana monkeys, which combine a contextually neutral initial 'A' call with one of three, 'H', 'L', or 'R', calls related to ongoing behaviour or external events (Candiotti et al. 2012). The initial 'A' , similar to our close calls, potentially functions as an individual identifier (Candiotti et al. 2012).

Even though the exact function of the non-random concatenation of calls in the context of affiliation remains unclear, it is clear that the behaviour can significantly enlarge the vocal repertoire of a species (Candiotti et al. 2012). Similar to the social calls in Diana monkeys (Candiotti et al. 2012) and the food calls in bonobos (Clay and Zuberbühler 2011), the call sequences in banded mongooses show that animals appear to attend to sequences to make inferences about the current situation experienced by the caller in a non-dangerous situation.

Traditionally, the number of discrete sounds is the conventional technique of estimating vocal repertoire sizes, but there is a growing body of evidence that compositionality (be it of calls, elements, or syllables) and vocal cues are communicatively relevant. Especially if such additional dimensions of information coding are also relevant for contexts other than the one of alarm calls or general danger, such combinatorial properties may be more widespread in animal communication than previously thought. Simply accounting for the number of discrete calls may largely underestimate the communicative capacity of a species. However, it remains problematic that relatively little is known about the meaningful informational content of such additional dimensions (Zuberbühler 2002; Ouattara et al. 2009a; Lemasson and Hausberger 2011). Especially in relation to social or affiliative calls, the elaborated number of associated contexts and acoustic structures often affects the investigations (Lemasson and Hausberger 2011).

Although the recent studies on call combinations and other dimensions of information encoding have offered a new perspective for comparisons of human language and animal vocal communication, animal signals also need to be interpreted in relation to the species' ecology and social structures (Fitch 2012). This study adds to the recent insights into the mechanisms animals use to overcome the anatomical constraints in the number of different calls they can produce. This is something that might especially be important in species which strongly depend on vocal signals to coordinate behaviours and maintain group cohesion. More elaborated studies that include playback experiments will be needed to uncover the potential information hidden in, often frequently used, vocalisations in the social and close distance vocal communication. A better understanding of affiliative signals may not only shed light on the evolution of animal signals, but may also enable us to better understand the social dynamics of species.

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References

Altman, J (1974). "Observational study of behavior: sampling methods". *Behaviour*, 49, 227–267.

Arnold, K and K Zuberbühler (2006). "Language evolution: Semantic combinations in primate calls". *Nature*, 441(7091), 303.

— (2008). "Meaningful call combinations in a non-human primate". *Current Biology*, 18(5), R202–R203.

ASAB (2006). "Guidelines for the treatment of animals in behavioural research and teaching". *Animal behaviour*, 71(1), 245–253.

Bates, DM (2011). *lme4: Mixed-effects modeling with R*. New York: Springer.

Bell, MBV (2007). "Cooperative begging in banded mongoose pups". *Current Biology*, 17(8), 717–721.

Blumstein, DT and KB Armitage (1997). "Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls". *American Naturalist*, 150(2), 179–200.

Boughman, JW and GS Wilkinson (1998). "Greater spear-nosed bats discriminate group mates by vocalizations". *Animal Behaviour*, 55(6), 1717–1732.

Candiotti, A, K Zuberbühler, and A Lemasson (2012). "Context-related call combinations in female Diana monkeys". *Animal Cognition*, 15(3), 327–339.

Cant, MA (1998). "Communal breeding in banded mongooses and the theory of reproductive skew". PhD thesis. Cambridge, UK: University of Cambridge.

— (2000). "Social control of reproduction in banded mongooses". *Animal Behaviour*, 59(1), 147–158.

Charrier, I, T Aubin, and Mathevon (2010). "Mother-Calf vocal communication in Atlantic walrus: a first field experiment". *Animal Cognition*, 13(3), 471–482.

Clarke, E, UH Reichard, and K Zuberbühler (2006). "The syntax and meaning of wild gibbon songs". *PLoS ONE*, 1(1), e73.

Clay, Z and K Zuberbühler (2011). "Bonobos extract meaning from call sequenses". *PLoS ONE*, 6(4), e18786.

Crockford, C and C Boesch (2005). "Call combinations in wild chimpanzees". *Behaviour*, 142, 397–421.

DaCunha, RGT and RW Byrne (2008). "The use of vocal communication in keeping the spatial cohesion of groups: intentionality and specific functions". In: *South American primates: comparative perspectives in the study of behavior, ecology, and conservation*. Ed. by PA Garber et al. New York: Springer, pp. 341–363.

Endress, AD et al. (2009). "Evidence of an evolutionary precursor to human language affixation in a non-human primate". *Biology Letters*, 5(6), 749–751.

Fairbanks, BM, KS Alexander, and DM Hawley (2011). "Leadership Behavior in Banded Mongooses (*Mungos mungo*)". *Integrative and Comparative Biology*, 51, E188–E188.

Fischer, J and K Hammerschmidt (2002). "An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire." *Folia Primatologica*, 73(1), 32–45.

Fitch, TW (2012). "Segmental structure in banded mongoose calls". *BMC Biology*, 10(98).

Fitch, WT (2000). "Skull dimensions in relation to body size in nonhuman primates: the causal bases for acoustic allometry." *Zoology*, 103(1-2), 40–58.

Furrer, RD (2009). "Leadership and group-decision-making in banded mongooses (*Mungos mungo*)". PhD thesis. Zurich, Switzerland: University of Zurich.

Furrer, RD and MB Manser (2009). "The Evolution of Urgency-Based and Functionally Referential Alarm Calls in Ground-Dwelling Species". *American Naturalist*, 173(3), 400–410.

Furrer, RD et al. (2011). "Location and group size influence decisions in simulated intergroup encounters in banded mongooses". *Behavioral Ecology*, 22(3), 493–500.

Gilchrist, JS (2004). "Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance". *Behavioral Ecology*, 15(6), 952–960.

Green, S (1975). "Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study". *Primate Behavior, Developments in Field and Laboratory Research*, 2, 1–102.

Gustison, ML, A le Roux, and TJ Bergman (2012). "Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1847–1859.

Harcourt, AH, KJ Stewart, and MD Hauser (1993). "Functions of wild gorilla 'close' calls. 1. repertoire, context, and interspecific comparison". *Behaviour*, 124, 89–112.

— (1996). "Functions and meaning of wild gorilla 'close' calls. 2. Correlations with rank and relatedness". *Behaviour*, 133, 827–845.

Heiberger, RM and B Holland (2004). *Statistical Analysis and Data Display: An Intermediate Course with Examples in S-Plus, R, and SAS*. Springer Texts in Statistics.

Heiberger, RM (2012). *HH: Statistical Analysis and Data Display: Heiberger and Holland*. R package version 2.3-27.

Jameson, JW and JF Hare (2009). "Group-specific signatures in the echolocation calls of female little brown bats (*Myotis lucifugus*) are not an artefact of clutter at the roost entrance". *Acta Chiropterologica*, 11, 163–172.

Jansen, DAWAM (2013). "Vocal communication in the banded mongoose (*Mungos mungo*)". PhD thesis. University of Zurich.

Jansen, DAWAM, MA Cant, and MB Manser (2012). "Segmental concatenation of individual signatures and context cues in banded mongoose *Mungos mungo* close calls". *BMC Biology*, 10(97).

Jordan, NR et al. (2010). "Scent marking within and between groups of wild banded mongooses". *Journal of Zoology*, 280(1), 72–83.

Kondo, N and S Watanabe (2009). "Contact calls: Information and social function". *Japanese Psychological Research*, 51(3), 197–208.

Lemasson, A and M Hausberger (2011). "Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*)". *Journal of the Acoustical Society of America*, 129(5), 3341–3352.

McComb, K and S Semple (2005). "Co-evolution of vocal communication and sociality in primates". *Biology Letters*, 1(4), 381–385.

Messeri, P et al. (1987). "A study of the vocal repetoire of the banded mongoose (*Mungos mungo*)". *Italian journal of Zoology*, 19(22), 341–73.

Metherell, B (2009). "Offspring care and communication in the banded mongoose". PhD thesis. Cambridge, UK: University of Cambridge.

Müller, CA and MB Manser (2007). "'Nasty neighbours' rather than 'dear enemies' in a social carnivore". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 274(1612), 959–965.

— (2008). "Mutual recognition of pups and providers in the cooperatively breeding banded mongoose". *Animal Behaviour*, 75(5), 1683–1692.

Mundry, R and C Sommer (2007). "Discriminant function analysis with nonindependent data: consequences and an alternative". *Animal Behaviour*, 74(4), 965–976.

Ouattara, K, A Lemasson, and K Zuberbühler (2009b). "Campbell's Monkeys Use Affixation to Alter Call Meaning". *PLoS ONE*, 4(11), e7808.

— (2009a). "Campbell's monkeys concatenate vocalizations into context-specific call sequences". *Proceedings of the National Academy of Sciences of the United States of America*, 106(51), 22026–22031.

Owren, MJ, RM Seyfarth, and DL Cheney (1997). "The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): Implications for production processes and functions". *Journal of the Acoustical Society of America*, 101(1), 2951–2963.

R Core Team (2012). *R: A Language and Environment for Statistical Computing*. ISBN 3-900051-07-0. R Foundation for Statistical Computing. Vienna, Austria.

Radford, AN and AR Ridley (2007). "Individuals in foraging groups may use vocal cues when assessing their need for anti-predator vigilance". *Biology Letters*, 3(3), 249–252.

Reber, S, SWT Townsend, and MB Manser (in review). "Social monitoring via close calls in meerkats allows for flexible responses depending on relationship quality." *Proceedings of the Royal Society of London Series B-Biological Sciences*.

Rendall, D (2003). "Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons." *Journal of the Acoustical Society of America*, 113(6), 3390–3402.

Rendall, D and MJ Owren (2002). "Animal Vocal Communication: Say what?" In: *The cognitive animal: Emperical and Theoretical Perspectives of Animal Cognition*. Ed. by M Bekoff, C Allen, and G Burghart. Cambridge, MA: MIT press, pp. 1–17.

Rendall, D et al. (1999). "The meaning and function of grunt variants in baboons". *Animal Behaviour*, 57(3), 583–592.

Rood, JP (1974). "Banded Mongoose Males Guard Young". *Nature*, 248(5444), 176–176.

— (1983). "Banded Mongoose Rescues Pack Member from Eagle". *Animal Behaviour*, 31(11), 1261–1262.

Schel, AM, S Tranquilli, and K Zuberbühler (2009). "The alarm call system of two species of black-and-white colobus monkeys (*Colobus polykomos* and *Colobus guereza*)". *Journal of Comparative Psychology*, 123(2), 136–150.

Schrader, L and K Hammerschmidt (1997). "Computer-aided analysis of acoustic parameters in animal vocalizations: a multi-parametric approach." *Bioacoustics*, 7(4), 247–265.

Shapiro, AD (2010). "Recognition of individuals withing social group: signature vocalizations". In: *Handbook of mammalian vocalization*. Ed. by SM Brudzynski. Oxford: Elsevier Academic Press, pp. 495–503.

Slocombe, KE and K Zuberbühler (2007). "Chimpanzees modify recruitment screams as a function of audience composition". *Proceedings of the National Academy of Sciences of the United States of America*, 104(43), 17228–17233.

Specht, R (2012). *Avisoft SASLab Pro. User's Guide for version 5.2*. Avisoft Bioacoustics. Berlin.

Townsend, SW, C Allen, and MB Manser (2012). "A simple test of vocal individual recognition in wild meerkats". *Biology Letters*, 8(2), 179–182.

Townsend, SW, LI Hollen, and MB Manser (2010). "Meerkat close calls encode group-specific signatures, but receivers fail to discriminate". *Animal Behaviour*, 80(1), 133–138.

Townsend, SW, M Zoettl, and MB Manser (2011). "All clear? Meerkats attend to contextual information in close calls to coordinate vigilance". *Behavioral Ecology and Sociobiology*, 65(10), 1927–1934.

Venables, WN and BD Ripley (2002). *Modern Applied Statistics with S*. 4th. Berlin Heidelberg: Springer.

Weihs, C et al. (2005). "klaR Analyzing German Business Cycles". In: *Data analysis and decision support*. Ed. by D Baier, R Decker, and L Schmidt-Thieme. Berlin: Springer, pp. 335–343.

Zuberbühler, K (2003). "Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language". *Advances in the Study of Behavior*, 33, 265–307.

Zuberbühler, K (2002). "A syntactic rule in forest monkey communication". *Animal Behaviour*, 63(2), 293–299.

4

Testing for vocal individual discrimination in adult banded mongooses

David A.W.A.M Jansen, Michael A. Cant. and Marta B. Manser. (resubmitted) **Testing for vocal individual discrimination in adult banded mongooses (*Mungos mungo*)** *Journal of Zoology*

Testing for vocal individual discrimination in adult banded mongooses

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Abstract

The ability to individually recognise conspecifics is acknowledged as one of the prerequisites for the development of sophisticated social relationships in group-living species. It has been hypothesised that the discrimination of individual identities is crucial for the maintenance of social relationships and cooperation based on repeated interactions, and for the evolution of many social behaviours. Previous studies have shown that the close calls of the cooperatively breeding banded mongoose (*Mungos mungo*) are individually distinct. For instance, banded mongoose pups are able to distinguish between close calls of their escort and of a non-escort. In this study we used playbacks based on the recently proposed violation-of-expectation paradigm and dominance/age class recognition to investigate whether adult banded mongooses use the individual signature of close calls to distinguish among adult group members. The individual signature in the close calls seemed not to be used to discriminate between group members in our test set-up among adult banded mongooses. Based on the previous work on banded mongoose pups we propose this is not due to an incapacity to do so, but more likely a lack of motivation, and no need or benefit to show a differentiated response. The study highlights the importance of understanding the function of a signal (e.g. the expected response), timing and the biology of the species when designing and performing playback experiments.

Keywords: close call, individual discrimination, violation-of-expectation, motivation, banded mongoose

Introduction

The ability to recognise characteristics such as sex, reproductive status, social rank, kinship, identity, group membership and/or familiarity of conspecifics is acknowledged as one of the prerequisites for the development of sophisticated social relationships (Sherman 1997; Bradbury and Vehrencamp 1998). Individual recognition of conspecifics is thought to play a major role for the maintenance of social relationships and cooperation based on repeated interactions among group members (Tibbetts and Dale 2007). It has been hypothesised to also be of vital importance for the evolution of many social behaviours (Hamilton 1971; Hauser 1996). Although individual discrimination is believed to be widespread in non-human animals (Tibbetts and Dale 2007; Seyfarth and Cheney 2009), it is hard to prove conclusively as it requires a demonstration that discrimination occurs at the level of the individual. Even more challenging is to demonstrate 'true' individual recognition, since one additionally has to prove that receivers match current sensory cues (e.g. sounds) with stored information (i.e. mental representations or templates) of the properties of a conspecific as well as of the identity of a specific individual (Zayan 1994; Tibbetts and Dale 2007). Recognition of individuals as belonging to a broader level of categories containing more than one individual, is termed 'class level' or 'social' recognition (hereafter class recognition; Mateo 2004; Tibbetts and Dale 2007).

While evidence to true individual vocal recognition is limited, several studies do provide evidence that non-primates animals like domestic horses (*Equus caballus*, Proops et al. 2009), spotted hyaenas (*Crocuta crocuta*, Benson-Amram et al. 2011); Greylag Geese (*Anser anser*, Scheiber et al. 2011); Jungle crows (*Corvus macrorhynchos*, Kondo et al. 2012); and meerkats, (*Suricata suricatta*, Townsend et al. 2012), recognise the identity of a specific individual through unique vocal properties of the conspecific. This may be due to the absence of the ability to recognise, but could also be caused by the lack of suitable test situations. With the possible exception of mother-offspring recognition and other third-party relationship recognition systems (Engh et al. 2005; Cheney and Seyfarth 2007), class recognition is sufficient for many interactions and there are only limited situations where individual recognition has a clear advantage over class recognition (Cheney and Seyfarth 2007; Tibbetts and Dale 2007). Additionally animals may only have limited motivation to show an obvious response (Fischer et al. 2001) or have a limited sensitivity period, when an individualistic response might be needed, for instance in a period of need or conflict (Steiger and Müller 2010; Reber et al. in review).

This is especially the case when looking at low arousal vocalisations such as growls or contact calls (Fischer et al. 2001; Townsend et al. 2012). Townsend and co-authors (2012) proposed a novel violation-of-expectation paradigm to test for individual recognition and to overcome some of these issues. Using a combination of congruent and incongruent playbacks they showed that meerkats individually discriminate group members. Together with an additional study on social monitoring of the behaviour of of dominants by subordinates in meerkats (Reber et al. in review), the study by Townsend and colleagues (2012) provide support for the use of vocalisations for individual recognition. They propose that the violation-of-expectation paradigm can be used in a range of species to test for individual discrimination.

Cooperatively breeding banded mongooses (*Mungos mungo*) are small ($\leq$ 2kg) social carnivores that show high group cohesion. They live in mixed sex groups which average around 20 individuals, but groups occasionally increase to more than 70 individuals (Cant 1998). They cooperate in pup care, predator avoidance and territory defence (Rood 1975; Cant 1998). Aggression within groups is usually low and restricted to competitions over food (Rood 1975; De Luca 1998). Increased level of competition among males is observed when females are in oestrus. During this period males exhibit a rather obvious dominance hierarchy when competing for access to females (Nichols et al. 2010). A, mostly age-based, hierarchy is formed among females, when older females enter oestrus a few days before younger females and occasionally evict younger group members (Cant 2000; Cant et al. 2010). Multiple adult females are involved in most breeding attempts (Cant et al. 2010). Both adult males and females are forcibly evicted from the group when their numbers grow large. Older females mainly initiate aggression towards younger females, followed by targeted aggression of other group members (Cant et al. 2010). During some periods of female evictions, males are also evicted (Cant and Field 2001).

Similar to other social group-living species, keeping track of conspecifics could be advantageous to coordinate behaviours and to avoid conflict. Banded mongooses use a range of vocalisations to coordinate behaviours and to maintain group cohesion (Messeri et al. 1987; Furrer 2009). Foraging banded mongooses move in and out of dense vegetation and they dig for food items in the soil with their head down. Besides digging they also search for food on the surface, this is mainly done in the thickets. They are therefore generally visually constrained during foraging and vocalizations likely play a critical role in keeping individuals informed of the social and ecological environment. Whilst foraging they frequently emit close calls (Fig. 1), which most likely function in the maintenance of group cohesion as described in

other species (Kondo and Watanabe 2009). The close calls of banded mongooses have been shown to be individually distinct (Müller and Manser 2008; Jansen et al. 2012). Banded mongoose pups are able to distinguish between playbacks of close calls of their escort and of a non-escort, suggesting that they are able to discriminate adult group members based on the individual signature in the close call (Müller and Manser 2008). However, it is unclear whether this vocal recognition also exists among adults. Despite that, in contrast to many other cooperatively breeding species, clear classes (e.g dominant versus subordinates) are absent, competition and conflict does occur and hierarchies are formed during periods of competition. They are therefore likely to show individual discrimination to facilitate for instance social monitoring. In this study we used the violation-of-expectation paradigm playback experiments based on Townsend and colleagues' study (2012), to test whether adult banded mongooses use the individual signature of close calls to distinguish among group members. Additionally we performed a conflict dominance/age class recognition (based on differences in dominance/age) playback experiment.

Figure 1. Typical example of a banded mongoose digging close call (Gauss, FTT = 1024, overlap=97.87%, frequency resolution = 43 Hz).

Materials and Methods

Study population

The study was performed at the Banded Mongoose Research Project, in the Queen Elizabeth National Park, Uganda (0°12S; 29°54E). Cant (1998) and Jordan et al. (2010) have described the study site and the habituated population in detail. During the 3 periods of data collection between February 2009 and August 2011, the study population consisted of four to six habituated groups and three semi-habituated groups, with group sizes ranging from 6 to over 50 (average 20 individuals). In four groups, most individuals were habituated to a level that allowed us to follow them with a microphone and to do detailed focal watches within 5 m.

Recording methods

All close calls used in the playback experiments were recorded from well-habituated adult (≥ 1 year) banded mongooses at a distance of approximately 1-2 m, using a Sennheiser directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40–20000 Hz ± 2.5 dB, sampling rate 16 bit, Old Lyme, Connecticut, U.S.A.) connected to a Marantz PMD-660 solid state recorder (Marantz Japan Inc.), or a M-Audio Microtrack II (Avid Technology USA Inc). Calls were recorded as

part of detailed behavioural focal watches or during *ad libitum* sampling recording sessions (Altman 1974).

Playback protocol

Calls used in playback experiments were randomly selected close calls of adult group members. For playbacks, calls with high signal-to-noise ratio were selected, using Cool Edit Pro 2000 (Syntrillium Software Corporation, Phoenix, AZ, US). Playback experiments were conducted on adult banded mongooses belonging to four different groups. During the experiments we kept track of the spatial position of the adults, whose calls were played back to ensure they were over 10m away from the test subject. Calls were then played back from a Marantz PMD-660 solid state or a M-Audio Microtrack through a loudspeaker (JBL on tour). The loudspeakers were attached to the lower leg of the observers at the height similar to that of the head of a foraging banded mongoose (5 to 10 cm above ground; Townsend et al. 2012; Reber et al. in review). Close calls are generally soft and, as the amplitude is often below that of background noise (e.g. bird song), it was not possible to use sound level meter. Calls were played back at natural occurring amplitudes estimated by hearing. A subject was followed until it was foraging at a clearly defined foraging spot (e.g. a pile of elephant dung), preferably in the open. Before the call was played back, we filmed using a digital camera (Canon HF100 or Toshiba Camileo S20) the behaviour of the subject for a minimum of 30 seconds. Thereafter we performed one of two different playback experiments. The playback was paused if the focal went out of sight, the group started moving or an alarm call was given. Only one playback experiment per focal was done per day and a minimum of three days separation was used between experiments to avoid habituation.

Playback 1 - Violation of expectation

We randomly selected digging close calls of two adult group members to create two playback conditions: a) control (congruent); and b) test (incongruent). Both conditions consisted of two playbacks containing three close calls each, which were separated by approximately three seconds (within natural calling rate of the banded mongoose; median = 12 per minute; range = 0 - 60; Jansen unpublished data). In the test condition, both playback files consisted of close calls recorded from the same individual. In the control condition, one playback file consisted of close calls (Fig. 1) from the same group member as used in the test condition and the second playback file consisted of close calls from a different group member. The test condition simulated a situation where an individual is foraging on one side of the subject and then a few seconds later appears on the opposite side, which is physically unlikely

(Fig. 2). By presenting subjects with different calls from the same individual, we ensured that any violation-of-expectation response in the incongruent condition would be based on the listener's recognition that the calls came from the same individual, not that they constituted the exact same stimulus (Townsend et al. 2012). During playbacks the first experimenter (DJ) was positioned approximately two meters from the subject and filmed the behaviour from close distance. The the second experimenter (KM) stood at approximately five meters from the subject and seven meters from the first experimenter, this to ensure a sufficient shift to induce the violation-of-expectation. These distances ensured that observer (DJ) had a clear view of the subject and could record all behaviours. The order of the distance, 2m versus 5m, that was first played back was randomized. The set-up of test and control conditions was kept the same and the order in which subjects heard the test or control conditions was randomised. In case the playback had to be paused, the experiment was restarted after a break of at least 30 minutes. Calls used for playbacks originated from 20 different individuals of these four groups (3 to 6 individuals per group).

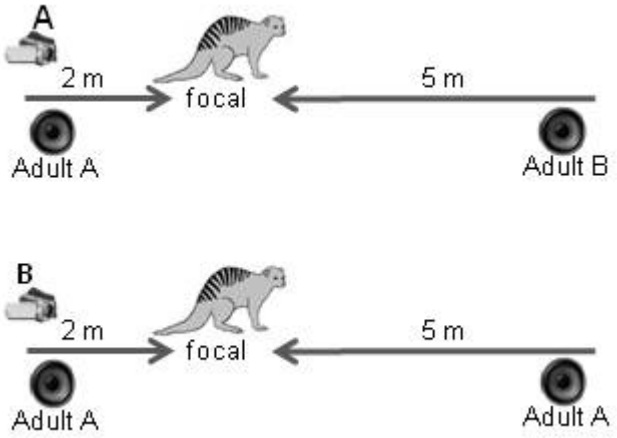

Figure 2. Playback protocol for Experiment 1. Protocol was used in both the (a) congruent (control) and (b) incongruent (test) conditions. Camera indicated position of observer (DJ) recording the behaviour of the focal.

Playback 2 - Class/age recognition

Playbacks were done with digging close calls of group members that belonged to one of the following dominance/age classes : a) likely to be higher in social hierarchy (i.e. more dominant and older); b) litter mate (same age); and c) likely to be lower in the social hierarchy (younger). Categorisation selection was based on behavioural observation in the few weeks prior to the playback. Behavioural

observations included aggression, submission, mating, attempts of eviction and outcomes of foraging competitions. In most cases older individuals were used as dominants and younger individuals as subordinates. We played back sets of three close calls of a group member of the same sex as the focal individual were selected per class. Close calls were separated by approximately three seconds. With sets of three calls we created blocks with calls of calls of individuals of the three different dominance classes/ages. The order of the classes within the blocks was randomised. All three possible orders were played back consecutively (e.g. $A-B-C$, $B-C-A$, $C-B-A$). Therefore the complete playback consisted of 27 calls. During playbacks the experimenter (DJ) was positioned approximately two meters from the focal subject and filmed behaviours from a close distance. Nineteen playback trials were performed with 16 different individuals from four different groups (2 to 5 focal individuals per group). Calls used for playbacks originated from 28 different individuals of these four groups.

Behavioural responses

We analysed videos using Media Player Classic (Sourceforge.net 2011). Close calls are a regularly emitted low-arousal state vocalisation and we therefore did not expect a strong response. We focused on vigilance behaviour and noted: a) each time the subject scanned the surrounding area and c) the duration of each vigilance bout (i.e. looking time). Behavioural responses were noted from the onset of the first call of the playback, up to five seconds after the last call.

Statistical analysis

All statistical analyses were done in R 2.15.2 using the R packages 'lme4' (Bates 2011), 'coin' (Hothorn et al. 2006) and 'AICcmodavg' (Mazerolle 2012). As the experimental setup of the first experiment (violation-of-expectation) followed a within-subject design and sample sizes were small, we used exact Wilcoxon signed-rank tests to analyse the effect of playback type (congruent or incongruent) on vigilance duration and number of looks. We computed 95% CI for effect sizes using a bootstrapping method with 10000 repetitions to establish the significance of our sample.

To investigate whether vigilance behaviour was affected by dominance category in the second experiment (dominance/age class recognition) we performed a series of generalized linear mixed models (GLMM) with a binomial (0 = no vigilance response, 1 = vigilance response) and Gaussian distribution (vigilance duration). The dominance/age class and the identity of the caller were included as fixed factors and the identity of the focal individual as a random factor. Due to the small sample sizes we used Akaike's second order information criteria (AICc) to select

the most plausible model (Mazerolle 2012). Lower AICc values correspond with better relative support for each model and terms were only kept in the model if their removal inflated AICc by more than two (Mazerolle 2012). The minimal model only consisted of an intercept and the random factor. To validate that there was no improvement to the minimal model, all original terms were returned to the model one by one, creating a model set together with the basic model, containing only the intercept and the random term.

Results

Violation of expectation

The response of the subjects to the congruent (control) and incongruent (test) conditions of the playbacks did not differ. Eight out of the 15 tested subjects showed a vigilance response during the control condition, whereas in the test condition this happened four times. There was no difference in vigilance behaviour between the control and the test conditions (number of looks: exact Wilcoxon test: $Z = -0.95$, $p = 0.40$, $n = 15$, $r = -0.16$; vigilance duration (s): $Z = -0.84$, $p = 0.43$, $n = 15$, $r = -0.14$). Baseline vigilance behaviour measured during the 30 sec. before the calls were played also did not differ between conditions (number of looks: $Z = 1.45$, $p = 0.33$, $n = 14$, $r = 0.16$; vigilance duration (s): $Z = 1.31$, $p = 0.33$, $n = 14$, $r = 0.16$; Table 1). Bootstrapping of the effect sizes and calculation of 95% confidence intervals verified that the reported effect sizes did not significantly differ from 0 and that our sample size was sufficiently large enough (Fig. 3).

Table 1. Overview of responses in the violation- of-expectation playback.

	Congruent		Incongruent	
Part	Looks	Duration (s)	Looks	Duration (s)
Before	1 (0 - 1)	0 (0 - 1)	1 (0 - 1)	0 (0 - 1)
After	0 (0 - 1)	0 (0 - 2)	0 (0 - 4)	0 (0 - 2)

Given are the median (range)

Class/Age recognition

Mongooses overall showed low vigilance behaviour during the playbacks testing a discrimination between members of different dominance/age classes (median number of looks: 3, $(range : 0 - 7)$, $n = 19$; median duration (s): 7, $(0 - 32.5)$, $n = 19$; see table 2 for responses per block). Thirteen individuals responded at least once during the playbacks (median number of looks: 4, $(1 - 7)$, $n = 19$; median duration

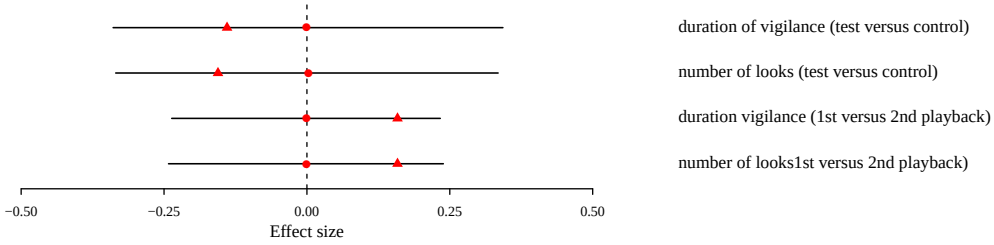

Figure 3. Summary of repeatability of effect estimations. i.) duration of vigilance in test versus control condition); ii.) number of looks in a) incongruent (test) versus b) congruent (control) condition; iii.) duration of vigilance in 1st playback versus 2nd playback. iv.) number of looks in 1st playback versus 2nd playback; The x-axis represents the effect size. Triangles are the computed estimates of effect based on our data. The solid circles represent the calculated mean effect based on bootstrapping. The horizontal lines represent the 95 % confidence intervals of the bootstrapped effect sizes.

(s): 8, $(1 - 32.5)$, $n = 19$). The likelihood of responding or vigilance duration was not affected by dominance or identity of caller (Table 3). For all test conditions the basic model that only contained the identity of the receiver as a random factor was the best model.

Table 2. Overview of responses per block in the dominance/age class recognition playback experiment.

Block	Class[1]	Looks	Duration
1	D	0 (0 - 1)	0 (0 - 4)
1	L	0 (0 - 1)	0 (0 - 5)
1	S	0 (0 - 1)	0 (0 - 23)
2	D	0 (0 - 1)	0 (0 - 4)
2	L	0 (0 - 1)	0 (0 - 6.5)
2	S	0 (0 - 1)	0 (0 - 9)
3	D	0 (0 - 1)	0 (0 - 9)
3	L	0 (0 - 1)	0 (0 - 0)
3	S	0 (0 - 1)	0 (0 - 4)

Given are the median (range)

[1] dominance/age class; D = Dominant (older); L = Litter mate (same); S = Subordinate (younger)

Table 3. GLMMs investigating the factors that predict the likelihood of vigilance duration and number of looks in a Class/Age recognition playback experiment.

		Duration		Looks	
Model	Description	AICc	Δ_i^a	AICc	Δ_i^a
	Basic[b]	1789	0	288	0
1	Full	1817	28	1744	1456
2	Dominance/age class only	1795	7	298	10
3	Caller ID only	1823	34	391	103

[a] $\Delta_i = AICc_i$ - $AICc_{min}$

[b] Only contains intercept and the random factors

Discussion

In this study banded mongooses did not respond differently to close calls of different individuals or dominance/age class categories . This suggests that adult banded mongooses appear not to discriminate between individuals based on the individual signature that is present in the close calls. It could be that banded mongooses simply do not possess the ability to recognise individuals. This would be surprising as individuals forming pup-escort associations mutually discriminate each other from other group members (Müller and Manser 2008). Pups can discriminate between close calls of their escorts versus other escorting individuals in the group. Escorts showed increased responsiveness towards distress signals of their escorted pup versus a different pup. Whilst this ability could simply be based on familiarity, it nevertheless shows that banded mongooses have the cognitive ability to discriminate between individuals. Therefore other reasons seem more plausible for the lack of response to our playback experiments of close calls of group members to adult individuals.

Close calls of the banded mongoose are graded and besides an individual signature contain a temporally separated behavioural signature cue indicating whether the individual is 'digging', 'searching' or 'moving' (Jansen et al. 2012). In this experiment we used 'digging' close calls as stimuli during playbacks. We used digging calls as the calls are emitted by individuals that are stationary and digging for food items. The individual signature in the banded mongoose close calls is encoded only in the initial noisy part of the close calls. The harmonic extension indicting the behaviour is not individually distinct (Jansen et al. 2012). The 'digging' close calls consist only of the initial noisy part and no harmonic extension. The 'searching' or 'moving' are not more individually distinct, but include additional information regarding the current behaviour of the caller(Jansen et al. 2012). We

therefore don't expect that a more individualistic response would have been shown to these variations.

A lack of response by the receivers may rather reflect a lack of motivation than an inability to discriminate between specific individuals. Close calls are frequently emitted during social foraging and are of low arousal. Therefore, upon hearing a close call the receiver in many cases may just acknowledge the presence of a group member without the need to respond, visually or vocally, to such a low arousal call. A similar pattern of an infants' ability to discriminate between calls, but lack of response in adults was observed in chacma baboons (*Papio cynocephalus ursinus*). Infant baboons discriminated between the commonly used graded bark variations; the intermediate alarm barks and clear contact barks (Fischer et al. 2000). Adult chacma baboons, however, failed to show a difference in response between these two call variations (Fischer et al. 2001). As infants were able to discriminate, the authors suggest that the lack of response is rather a lack of motivation than an inability to do so (Fischer et al. 2001).

The lack of motivation to respond may differ for the two playback experiments we conducted in the banded mongoose. The setup of the first experiment (violation-of-expectation paradigm) is based on the fact that the sudden shift of position of the caller violates the expectation of the receiver (Townsend et al. 2012). Banded mongooses, however, often forage in dense vegetation with many position shifts, both in distance to nearest neighbour and in relative position within the group (Rood 1975; Bell 2006). Therefore sudden shifts in position might not be a violation-of-expectation for a foraging banded mongoose, in the way it appears to be for the closely related meerkat (Townsend et al. 2012). This does not exclude that banded mongoose may not also socially monitor the position of other group members by their vocalisations.

The lack of response to the dominance/age class recognition playback may be based on the fact that a response to close calls may only be beneficial during specific periods of conflict or other socially relevant times. For example, adult subordinate female meerkats recognise the dominant female vocally based on close calls. However, test subjects only show a response to these calls when they are under threat of eviction, and not during non-conflict periods (Reber et al. in review). It is very likely that such sensitivity periods are also present in the banded mongoose. In the daily life of a group, conflict is likely to be limited to competitions over food (Rood 1975; De Luca 1998). Mongooses frequently forage on large ungulate dung piles. These piles are meticulously taken apart in search of dung beetles and their larvae. Especially the presence of fresh elephant (*Loxodonta*

africana) dung can lead to high congregation of mongooses, leading to high levels of foraging competition (Rood 1975). Occasionally higher levels of aggression do occur. Males for instance compete for access to females during oestrus, while both sexes occasionally aggressively evict mostly younger group members during periods of oestrus or early pregnancies (Cant et al. 2010; Nichols et al. 2010). In these periods of aggression it could be beneficial to be able to keep track of conspecifics.

We performed our playback experiments during normal foraging behaviour in periods with no breeding or extensive aggression in the group. We therefore might have been outside the sensitivity period, in which it would be beneficial for adult banded mongooses to discriminate between group members. However during for instance periods of oestrus, increased aggression or eviction many individuals spend little time continuously foraging and therefore experiments with the current set-up are extremely difficult. Also in certain non- or reduced conflict situations it can be beneficial to distinguish between group members

Bates et al. (2008) used a expectancy-violation paradigm experiment to investigate if African elephants monitor the location of conspecifics. Using urine samples they show that adult females show an increased response in situation of encountering cues of group members that are either absent or located behind the focal individual (Bates et al. 2008). Future research could attempt to investigate if banded mongooses monitor the location of conspecifics use a similar expectancy-violation paradigm experiment. During evictions group members are either temporally or permanently evicted from their natal group (Cant and Field 2001; Cant et al. 2010). During these evictions playbacks of close calls could be used to investigate if adults group members recognize group members.

In conclusion our results did not show that the individual signature in the close calls is used on a day-to-day basis in adult banded mongooses. This seems surprising considering the earlier findings that banded mongoose pups are able to distinguish adults based on their close calls. A lack in response to the playback of signals does not necessarily mean that the cognitive capacity is absent, it rather may indicate a lack of motivation or need to respond. It is possible that adults use the signature in specific situations (i.e. as the pups do in the pup-escort associations; Müller and Manser 2008) or during socially sensitive periods, like in periods of targeted aggression during eviction or oestrus. The lack of response in adult banded mongooses to close calls highlights the importance of understanding the function of a signal (e.g. its expected response) and its timing (i.e. aiming for the sensitivity period)

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References

Altman, J (1974). "Observational study of behavior: sampling methods". *Behaviour*, 49, 227–267.

Bates, DM (2011). *lme4: Mixed-effects modeling with R*. New York: Springer.

Bates, SW et al. (2008). "African elephants have expectations about the locations of out-of-sight family members". *Biology Letters*, 4(1), 34–36.

Bell, MBV (2006). "Communication, cooperation and conflict in banded mongooses." PhD thesis. Cambridge, UK: University of Cambridge.

Benson-Amram, S et al. (2011). "Numerical assessment and individual call discrimination by wild spotted hyaenas, *Crocuta crocuta*". *Animal Behaviour*, 82(4), 743–752.

Bradbury, JW and SL Vehrencamp (1998). *Principles of animal communication*. New York: Sinauer Associates.

Cant, MA (1998). "Communal breeding in banded mongooses and the theory of reproductive skew". PhD thesis. Cambridge, UK: University of Cambridge.

— (2000). "Social control of reproduction in banded mongooses". *Animal Behaviour*, 59(1), 147–158.

Cant, MA and J Field (2001). "Helping effort and future fitness in cooperative animal societies". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268(1479), 1959–1964.

Cant, MA et al. (2010). "Reproductive control via eviction (but not the threat of eviction) in banded mongooses". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 277(1691), 2219–2226.

Cheney, DL and RM Seyfarth (2007). *Baboon Metaphysics: the Evolution of a Social Mind*. Chicago: The university of Chicago press.

De Luca, DW (1998). "The socio-ecology of a plural breeding species: the banded mongoose, *Mungos mungo*, in Queen Elizabeth National Park, Uganda". PhD thesis. London, UK: University of London.

Engh, AL et al. (2005). "Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships". *Animal Behaviour*, 69(1), 209–217.

Fischer, J, DL Cheney, and RM Seyfarth (2000). "Development of infant baboons' responses to graded bark variants." *Proceedings of the Royal Society of London Series B-Biological Sciences*, 267(1459), 2317–2321.

Fischer, J et al. (2001). "Baboon responses to graded bark variants". *Animal Behaviour*, 61(5), 925–931.

Furrer, RD (2009). "Leadership and group-decision-making in banded mongooses (*Mungos mungo*)". PhD thesis. Zurich, Switzerland: University of Zurich.

Hamilton, WD (1971). "Geometry for the selfish herd". *Journal of Theoretical Biology*, 31, 295–311.

Hauser, MD (1996). *The evolution of communication*. Cambridge, MA: MIT Press.

Hothorn, T et al. (2006). "A Lego System for Conditional Inference." *The American Statistician* (3), 257–263.

Jansen, DAWAM, MA Cant, and MB Manser (2012). "Segmental concatenation of individual signatures and context cues in banded mongoose *Mungos mungo* close calls". *BMC Biology*, 10(97).

Jordan, NR et al. (2010). "Scent marking within and between groups of wild banded mongooses". *Journal of Zoology*, 280(1), 72–83.

Kondo, N and S Watanabe (2009). "Contact calls: Information and social function". *Japanese Psychological Research*, 51(3), 197–208.

Kondo, N, EI Izawa, and S Watanabe (2012). "Crows cross-modally recognize group members but not non-group members". *Proceedings of the Royal Society B: Biological Sciences*.

Mateo, JM (2004). "Recognition systems and biological organization: The perception component of social recognition". *Annales Zoologici Fennici*, 41(6), 729–745.

Mazerolle, MJ (2012). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 1.26.

Messeri, P et al. (1987). "A study of the vocal repetoire of the banded mongoose (*Mungos mungo*)". *Italian journal of Zoology*, 19(22), 341–73.

Müller, CA and MB Manser (2008). "Mutual recognition of pups and providers in the cooperatively breeding banded mongoose". *Animal Behaviour*, 75(5), 1683–1692.

Nichols, HJ et al. (2010). "Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose". *Animal Behaviour*, 80(4), 649–657.

Proops, L, K McComb, and D Reby (2009). "Cross-modal individual recognition in domestic horses (*Equus caballus*)". *Proceedings of the National Academy of Sciences of the United States of America*, 106(3), 947–951.

Reber, S, SWT Townsend, and MB Manser (in review). "Social monitoring via close calls in meerkats allows for flexible responses depending on relationship quality." *Proceedings of the Royal Society of London Series B-Biological Sciences*.

Rood, JP (1975). "Population dynamics and food habits of the banded mongoose". *East Africa Wildlife journal*, 13, 89–111.

Scheiber, I et al. (2011). "Juvenile Greylag Geese (*Anser anser*) Discriminate between Individual Siblings". *PLoS ONE*, 6(8), e22853.

Seyfarth, RM and DL Cheney (2009). "Seeing who we hear and hearing who we see". *Proceedings of the National Academy of Sciences of the United States of America*, 106(3), 669–670.

Sherman, PW (1997). "Recognition systems". In: *Behavioural Ecology: An Evolutionary Approach*. Ed. by J Krebs and N Davies. Blackwell Science, pp. 69–96.

Steiger, S and JK Müller (2010). "From class-specific to individual discrimination: acceptance threshold changes with risk in the partner recognition system of the burying beetle *Nicrophorus vespilloides*". *Animal behaviour*, 80(4), 607–613.

Tibbetts, EA and J Dale (2007). "Individual recognition: it is good to be different". *Trends in Ecology & Evolution*, 22(10), 529–537.

Townsend, SW, C Allen, and MB Manser (2012). "A simple test of vocal individual recognition in wild meerkats". *Biology Letters*, 8(2), 179–182.

Zayan, R (1994). "Mental representations in the recognition of conspecific individuals". *Behavioural Processes*, 33, 333–246.

General discussion

General discussion

Social complexity has been argued to drive the evolution of vocal repertoire size (i.e. vocal complexity hypothesis, Blumstein and Armitage 1997b; McComb and Semple 2005; Burkart and Schaik 2010; Freeberg et al. 2012). But this predicted increase is constrained by anatomical limitations in most species (Fitch 2000; Hammerschmidt and Fischer 2008) and this ultimately limits the sizes of species' vocal repertoires. To overcome this constraint animals have to use other mechanisms to increase variation in vocal expression and the potential of information available to receivers. Such flexibility in vocal production has been demonstrated in some species in a number of recent studies. The four preceding data chapters in this thesis deal with a range of such mechanisms of vocal production flexibility in the banded mongooses (*Mungos mungo*). I first described the vocal repertoire of a wild population of banded mongoose in their natural habitat by relating call types to the contexts they were emitted in. The fit to some of the predictions of the Morton motivational rules is also discussed. I then investigated the use of vocal cues in the frequently emitted close call and showed that banded mongooses convey multiple vocal cues in a 'simple' single syllable vocalisations, by the use of temporal segregation. This may likely be a way to avoid the problem of conveying multiple signatures in an ultimately constrained acoustic space. Temporal segregation of vocal cues as described for the banded mongoose, and also existent in other species, can be regarded as an extra dimension in the complexity of information coding in animal vocalisations. Furthermore, I showed that these close calls are used in non-random sequences in various affiliative contexts, demonstrating that such sequences are not only used in contexts related to danger. The playback experiments to investigate the use of the individual identity cues in the close calls did not show discrimination, which is likely due to a lack of motivation to show an obvious response in the tested situation.

In this concluding chapter, I discuss the consequences of our knowledge on the dimensions of acoustic variation potentially conveying information to receivers on the studies investigating the relationship between social complexity and vocal complexity. I highlight the diversity in vocal repertoires and the consequences this has on comparative studies. Finally I will give some suggestions for further research on the vocal communication in banded mongooses in particular and also on animal vocal communication in general.

Flexibility in vocal production in the banded mongoose

In banded mongooses many of the call types appear to be graded (Messeri et al. 1987, Chapter 1,) or used in combinations (Chapter 3), which may explain the relatively low number of discrete call types within their vocal repertoire. Recruitment calls, for instance, are emitted in response to different stimulus types: *i.*) secondary predator cues; *ii.*) snakes; and *iii.*) members of rival groups and eliciting of calls leads to group recruitment (Furrer and Manser 2009). Receivers responded faster to playbacks of high urgency calls related to snakes and rival mongooses, than to low urgency calls produced in response to faeces (Furrer and Manser 2009). These results suggest that the variation provides meaningful information for receivers regarding the level of urgency the caller is experiencing. Behavioural observations (pers. obs. David Jansen) suggest that such urgency or level of arousal differences also exist in other call types, such as alarm calls, screams of females under attack or lost calls.

The banded mongoose close calls combine cues for both individuality and behavioural context. Individual distinctiveness of calls in itself is not a rare phenomenon in animal vocalisations (Shapiro 2010). However in most cases individual cues are fused with other contextual information. The banded mongoose close call provides an example of a discrete individual 'segment' in a graded call containing information regarding individuality. The noisy, yet stable, segment of the close call, explained almost as much individual variation as the whole call. This implies that, despite the graded nature of the close call, individual identity is conveyed in a discrete way. This is likely not unique to the banded mongoose, but rather the consequence of analysing the variation in acoustics on a different level (i.e. within a single syllable) than in most other studies.

In most other animal communication studies the lowest unit analysed is the syllable. Besides the combination of words into sentences and syllables into words, humans also combine discrete units (i.e. vowels and consonants) into single syllables (Hauser and Fitch 2003; Fitch 2012). Such within-syllable encoding, through combination of stop consonant and vowels, generates syllables with different meanings. Consequently, combination of a stop consonant like /d/ versus /t/ combined with vowels like /e/ or /o/ create a richer signalling unit than each class (that is, stop consonant or vowel) alone could provide. Such segmental concatenation (versus 'syntactic' concatenation of syllables and words) are a core feature of the phonological component of human spoken language (Hauser and Fitch 2003).

While many non-humans animals use syllable combinations to convey information to receivers (birdsong, Marler and Slabbekoorn 2004; Berwick et al. 2011; rock hyraxes, *Procavia capensis*, Koren and Geffen 2009; or cetacean species, Payne and McVay 1971; Ford 1989), evidence for segmental concatenation in animals has not explicitly been described. The close call of the banded mongoose with a short uninterrupted call (≈ syllable) that contains a stable noisy segment followed by a variable harmonic extension (Chapter 2), appears to be analogous to this system. Through temporal segmentation banded mongooses convey multiple vocal cues in the call. These results show that segmental concatenation can also be present in animals. Banded mongooses are likely not unique in this and reviewing literature for call descriptions and spectrograms of vocalisations suggest that segmental segmentation is also be present in other species (Jansen et al. 2012).

The temporal or spectral segregation could enable species to increase the reliability of vocal cues, thereby the potential information for receivers, in their vocalisations. Especially species with graded call types would benefit from such systems as it would potentially enable receivers to reliably categorize these graded signals into discrete units (Harnad 1987). As vocal cues predominantly convey individual related cues of the sender, temporal segregation would therefore be predicted to evolve if signallers benefit from unambiguous multiple vocal cues (Jansen et al. 2012). Such positive selective benefits for receivers may particularly be occurring in affiliative contexts, where receivers are more likely to show a discriminate response based on the identity (or other characteristic) of the signaller. Meerkats (*Suricata suricatta*), for instance, respond to individual differences in close calls (Townsend et al. 2012), but in the context of alarm calls individual discrimination appears irrelevant (Schibler and Manser 2007). Studies on the presence of vocal cues often are associated with affiliative calls (i.e. contact calls) and are much less prevalent in the avoidance of predation context (Snowdon et al. 1997; Lemasson and Hausberger 2011, but see Cheney and Seyfarth 1988; Pollar 2011).

Call combinations in animals are often seen as possible insights into the 'fossils' of the evolution of human language (Jackendoff 1999) and therefore get cited in relation to semantically combinatorial syntax and possible links to the evolution of human language (Jackendoff 1999; Hurford 2011). However, these call combinations may also provide valuable insight into animal vocal communication in general. Through a non-random concatenation of calls, the range of potential information available to receivers can be increased (Zuberbühler 2002; Crockford and Boesch 2005; Arnold and Zuberbühler 2006; Arnold and Zuberbühler 2008). Evidence for such meaningful sequential structures in the affiliative context is limited, even though it has been hypothesised that such sequences should be prevalent in this context

(Snowdon et al. 1997; Lemasson and Hausberger 2011) as affiliative and agnostic call types are generally targeted more towards specific receivers and therefore may require more adaptation (≈ flexibility) depending in the social partners' calls or behaviour.

Banded mongooses emit varieties of call sequences in different contexts, including excitement over wet ground or onset of rain, initiation of group departure or leading the group, and having lost contact with the social group (Chapter 3). Thereby, the banded mongooses emit context-specific elements that are preceded by a close call. These findings provide evidence that such combinatorial sequences are also important outside the context of predation. The combination with the individually distinct close calls raises the question on how their vocal cues affect the meaning of the sequences. Similarly as suggested for the preceding 'A' calls in call sequences emitted by female Diana monkeys (*Cercopithecus diana*, Candiotti et al. 2012), they could function as individual identifiers. Individual identity is likely to play a more important role in affiliative contexts than in the context of predation (Snowdon et al. 1997; Lemasson and Hausberger 2011, but see Pollar 2011).

Whilst humans are among the most socially complex species, the number of contrasting sound segments (e.g. discrete units) in human spoken language is also constrained. Depending on the language the number of discrete sounds varies from around one dozen to several dozens (Nettle 2012). The vocal repertoire of a English speaker, if simply classified as the number of discrete sounds, would be a mere 26. A more extreme example for the use of limited number of discrete units are the native Hawaiians using a language that is made up from a mere five vowels and eight consonants (Schütz 1981). This would indicate a vocal repertoire size of 26 and 13 for the English and Hawaiian language, respectively. Although this is clearly a gross underestimate of the richness of human language, the number of discrete sounds is the conventional technique of estimating vocal repertoire sizes (Blumstein and Armitage 1997b; McComb and Semple 2005; Gustison et al. 2012). The seemingly infinity of human language is achieved by the systematic organization of sounds, both at the phonological level of syllables to create words and at the lexical syntax level to produce new meanings and sentences (Fitch 2012). This systematic organization of sounds can be seen as a mechanism to increase the acoustic variability of human sound production and the combinations of sounds are a core component of the human spoken language (Marler 1977; Fitch 2012; Nettle 2012). But 'similar' mechanism enable animals to increase the acoustic variation in their vocal repertoire and thereby the potentially increasing their capacity to convey information to receivers are often neglected in comparative studies. However, in the last 20 years, multiple studies have demonstrated these mechanisms are present

in many species and that they are meaningful to receives. Comparative studies should therefore not look at the number of different call types *per se*, but rather at the potential amount of information receivers could perceive from these call types.

Social complexity and vocal repertoires

To make conclusions on the effect of social complexity on vocal complexity, the predictions of increased vocal repertoires need to be controlled for differences in the habitat of a particular species. Simply looking at call types, one difference between the banded mongoose and two of the other group-living mongoose species, the dwarf mongoose (*Helogale parvula,* Rasa 1986) and meerkats (Manser 1999), is the absence of 'sentinel' calls in the banded mongoose, since they do not show pronounced sentinel behaviour. This is likely linked to differences in habitat. Therefore it is not a 'misfit' of the vocal complexity hypothesis. A sentinel call is also absent in the yellow mongoose (*Cynictis penicillata*), however here it is likely due to differences in the social system (LeRoux et al. 2009). As this species forages solitarily, the need to coordinate group movement is absent, and therefore it is not surprising that call types related to this behaviour are absent. Other differences in the vocal repertoire could also be related to the facilitative sociality nature of this species. Compared to 'obligate' solitary mongoose species the yellow mongoose possesses a larger number of call types that were only used in friendly contexts (i.e. affiliative contexts, LeRoux et al. 2009).

To avoid the issue of pronounced differences in the vocal repertoire caused by ecological factors it may be better to make predictions related to call types that related to the increased sociality (e.g. calls in the social interaction context). The usefulness of this was demonstrated in a recent comparative study between two closely related primates species, the chacma (*Papio ursinus*) and gelada (*Theropithecus gelada*) baboons. These species differ both in their social structure as in the ecology of the habitat they inhabit. Males of chacma baboons primarily form short temporary relationships with females, while gelada males form harem-like long-term bonds with 2-12 females (Gustison et al. 2012). To sustain the long term relationships gelada males need to 'maintain' relationships with his females, therefore he is involved in more affiliative interactions with these females. While call types related to behaviours that both species showed were about the same, gelada baboons had more vocalisations, specifically in this affiliative context (Gustison et al. 2012). Such 'social' or 'affiliative' calls could be defined as calls that are to communicate with group members in a non-predator avoidance context (Lemasson and Hausberger 2011; Candiotti et al. 2012).

Earlier studies have shown that receivers pay attention to slight, often graded, variations within call types related to predatory contexts (yellow-bellied marmots, *Marmota flaviventris*, Blumstein and Armitage 1997a; meerkats, Manser 2001; red-fronted lemurs, *Eulemur rufifrons*, Fichtel and Hammerschmidt 2002; black-capped chickadees, *Poecile atricapillus*, Templeton et al. 2005; and in banded mongooses, Furrer and Manser 2009). The recent studies on prominently west African primate species have demonstrated that combinatorial properties are also present in this context (Zuberbühler 2002; Crockford and Boesch 2005; Arnold and Zuberbühler 2006; Arnold and Zuberbühler 2008). It has been hypothesised that in comparison to calls in a predatory avoidance contexts, calls in the affiliative context should show similar or even more pronounced signs of flexibility in vocal production in terms of sequential structures or 'meaningful' within-call variation (Snowdon et al. 1997; Lemasson and Hausberger 2011).

Various studies have found that animals produce vocalisations that vary according to the social contexts and these acoustic differences are 'meaningful' to receivers (e.g. Japanese macaque, *Macaca fuscata*, Green 1975; vervet monkey, *Chlorocebus pygerythrus*, Seyfarth 1984; pygmy marmoset, *Cebuella pygmaea*, Snowdon et al. 1997; chacma baboons, Owren et al. 1997; chimpanzees, *Pan troglodytes*, Slocombe and Zuberbühler 2007; and for non-primate examples, kangaroo rats, *Dipodomys spectabilis*, Randall 1994; and meerkats, Townsend et al. 2011). Affiliative calls are also hypothesised to be more likely to contain identity or social class related recognition cues (Snowdon et al. 1997; Lemasson and Hausberger 2011). The recent studies on chimpanzees (Crockford and Boesch 2005), bonobos (*Pan paniscus*, Clay and Zuberbühler 2011), and Diana monkeys (Candiotti et al. 2012), and now confirmed in the banded mongooses (Chapter 3) show that sequential structures also exist in the realm of affiliative vocalisations.

This emphasized that with a possible link between social complexity and affiliative calls (Gustison et al. 2012), mechanisms of flexibility of vocal production need to be considered when investigating vocal complexity. A basic property of vocal communication is that receivers can perceive the information that is embedded in vocalisations (Hauser 1996; Maynard-Smith and Harper 2003; Seyfarth et al. 2010). For this, vocalisations need to vary sufficiently and consistently for different information to be reliable. The various mechanisms of vocal flexibility discussed in this thesis do create such additional variation that potentially increased the amount of information that is available to receivers. Nevertheless these additional dimensions of vocal signal variabilities are not considered when comparing vocal repertoires. The vocal complexity hypothesis is based on the principle that an increasing amount of interactions and (social) behaviours goes along with an

increasing demand for information to coordinate these behaviours (Marler 1977; Hauser 1996). By only accounting for the number of call types and ignoring the dimensions vocal variability due to combinations of different vocal units with the potential of conveying specific information to the receivers may lead to an underestimation of the communicative capacities of a species. This may especially be true for species like the banded mongoose which have graded call types which likely have more potential information for receivers within call types.

Conclusions and future directions

Many species possess graded call types and/or show various degrees of flexibility in vocal production. Ignoring the potential information available to receivers that may be embedded in these call types would underestimate the communicative capacities of those species. Additionally, flexibility in vocal production increases the capacity of a species that may provide more information in their vocalisations. Here I showed that banded mongooses use various dimensions of acoustic variability to communicate. Two studies related to the frequently emitted 'simple' syllable close call of banded mongooses provide evidence for *i*.) segmental segregation in animal vocalisations; *ii*.) 'discrete' vocal cues in a graded vocalisation; and *iii*.) the combinatorial properties in affiliative contexts. Overall, this study sheds light on many aspects of vocal communication and particularly on the importance of understanding the variation that underlies the production of animal vocalisations. The ability to convey variation in vocalisations that allows receivers to perceive different information need to be better quantified to be able to test predictions such as the vocal complexity hypothesis. A better understanding of graded signalling systems and the information available to receivers of graded call types would therefore not only increase our understanding of vocal animal communication (Meise et al. 2011), but possibly also of the relationship between social complexity and vocal communication.

Many studies have shown that receivers can extract meaningful information from graded vocalisations. The mechanism that receivers use to deal with the ambiguity of graded signals is unclear. It has been suggested that receivers could to a degree resolve the ambiguity by meaningful within-category classification (i.e. discrete units; Marler and Mundinger 1975; Harnad 1987). It has been hypothesised that this perception of a graded continuum as a series of discrete categories was a crucial stage in the evolution of human language (Marler 1975; Marler 1976). The segmental segregation that was found in the close call of the banded mongoose may facilitate the ability of receivers to categorise the seemingly graded continuum

into perceptually discrete signals. Future studies investigating the presence of vocal cues should try to establish if these cues are concentrated in certain specific characteristics of the call.

The graded nature of the vocal repertoire of the banded mongoose in general and the close calls specifically may provide an ideal system to test some of these mechanisms. An extensive and detailed set of playbacks will be needed to determine how, and exactly what, information receivers can extract from these close calls and the combinations with other context related call structures. This would provide insight into the perception of graded vocalisations by receivers. Whilst the close call provides an interesting topic to investigate categorisation of graded signals, the low arousal level of the call will provide a challenge for playbacks studies (see chapter 4 for details). Other call types, or sequences, may be more suitable to test some of these predictions and functions. Preliminary observations suggest that receivers differentiate responses based on the identity of the caller upon hearing 'lead' or 'lost' calls (pers. obs. David Jansen). This is likely most prevalent in periods of conflict or need. Attempts should be undertaken to investigate the discriminating capacities of the banded mongoose during such periods, such as threat of eviction or conflict over mating opportunities. Playback experiments should be conducted to investigate the role of the close calls in this potential individual discrimination.

Mongooses have a wide range of different social systems and the vocal repertoire of several of the species are rather well known. They therefore are well suited to uncovering some of the evolutionary connections between sociality and vocal complexity. It might especially be interesting to look at call types used in the affiliative contexts as they are likely closely linked to the differences in social systems.

References

Arnold, K and K Zuberbühler (2006). "Language evolution: Semantic combinations in primate calls". *Nature*, 441(7091), 303.

— (2008). "Meaningful call combinations in a non-human primate". *Current Biology*, 18(5), R202–R203.

Berwick, RC et al. (2011). "Songs to syntax: the linguistics of birdsong". *Trends in Cognitive Sciences*, 15(3), 113–121.

Blumstein, DT and KB Armitage (1997a). "Alarm calling in yellow-bellied marmots .1. The meaning of situationally variable alarm calls". *Animal Behaviour*, 53(1), 143–171.

— (1997b). "Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls". *American Naturalist*, 150(2), 179–200.

Burkart, JM and CP van Schaik (2010). "Cognitive consequences of cooperative breeding in primates?" *Animal Cognition*, 13(1), 1–19.

Candiotti, A, K Zuberbühler, and A Lemasson (2012). "Context-related call combinations in female Diana monkeys". *Animal Cognition*, 15(3), 327–339.

Cheney, DL and RM Seyfarth (1988). "Assesment of meaning and detection of unreliable signals by vervet monkeys". *Animal Behaviour*, 36(2), 477–486.

Clay, Z and K Zuberbühler (2011). "Bonobos extract meaning from call sequenses". *PLoS ONE*, 6(4), e18786.

Crockford, C and C Boesch (2005). "Call combinations in wild chimpanzees". *Behaviour*, 142, 397–421.

Fichtel, C and K Hammerschmidt (2002). "Responses of redfronted lemurs to experimentally modified alarm calls: Evidence for urgency-based changes in call structure". *Ethology*, 108(9), 763–777.

Fitch, TW (2012). "Segmental structure in banded mongoose calls". *BMC Biology*, 10(98).

Fitch, WT (2000). "Skull dimensions in relation to body size in nonhuman primates: the causal bases for acoustic allometry." *Zoology*, 103(1-2), 40–58.

Ford, JKB (1989). "Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia". *Canadian journal of Zoology*, 67(3), 727–745.

Freeberg, TM, RIM Dunbar, and TJ Ord (2012). "Social complexity as a proximate and ultimate factor in communicative complexity". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1785–1801.

Furrer, RD and MB Manser (2009). "Banded mongoose recruitment calls convey information about risk and not stimulus type". *Animal Behaviour*, 78(1), 195–201.

Green, S (1975). "Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study". *Primate Behavior, Developments in Field and Laboratory Research*, 2, 1–102.

Gustison, ML, A le Roux, and TJ Bergman (2012). "Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates". *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1847–1859.

Hammerschmidt, K and J Fischer (2008). "Constraints in primate vocal production". In: *The evolution of communicative creativity: From fixed signals to contextual flexibility*. Ed. by U Griebel and K Oller. Cambridge, MA: The MIT Press, pp. 93–119.

Harnad, S (1987). *Categorical perception : the groundwork of cognition*. Cambridge, UK: Cambridge University Press.

Hauser, MD (1996). *The evolution of communication*. Cambridge, MA: MIT Press.

Hauser, MD and WT Fitch (2003). "Language Evolution: The States of the Art". In: *Language Evolution: The States of the Art*. Ed. by M Christiansen and S Kirby. Oxford: Oxford University Press. Chap. What Are the Uniquely Human Components of the Language Faculty?, pp. 317–337.

Hurford, JR (2011). *The Origins of Grammar.* Oxford, UK: Oxford.

Jackendoff, R (1999). "Possible stages in the evolution of the language capacity". *Trends In Cognitive Sciences*, 3, 272–279.

Jansen, DAWAM, MA Cant, and MB Manser (2012). "Segmental concatenation of individual signatures and context cues in banded mongoose *Mungos mungo* close calls". *BMC Biology*, 10(97).

Koren, L and E Geffen (2009). "Complex call in male rock hyrax: a multi-information distributing channel." *Behavioral Ecology and Sociobiology*, 63(4), 581–590.

Lemasson, A and M Hausberger (2011). "Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*)". *Journal of the Acoustical Society of America*, 129(5), 3341–3352.

LeRoux, A, MI Cherry, and MB Manser (2009). "The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality". *Naturwissenschaften*, 96(5), 575–584.

Manser, MB (1999). "Response of foraging group members to sentinel calls in suricates, Suricata suricatta". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 266(1423), 1013–1019.

— (2001). "The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency". *Proceedings of the Royal Society of London Series B-Biological Sciences*, 268(1483), 2315–2324.

Marler, P (1975). "On the origin of speech from animal sounds." In: *The role of speech in language*. Ed. by J Kavanagh and J Cutting. Cambridge, MA: MIT Press. Chap. On the origin of speech from animal sound, pp. 11–37.

— (1976). "Social organization, communication and graded signals the chimpanzee and the gorilla". In: *Growing points in ethology*. Ed. by PPG Bateson and RA Hinde. Cambridge: Cambridge University Press, pp. 239–281.

Marler, P (1977). "The evolution of communication". In: *How animals communicate*. Ed. by TA Sebeok. Bloomington: Indiana University Press, pp. 45–70.

Marler, P and PC Mundinger (1975). "Vocalizations, social-organization and breeding biology of twite *Acanthus flavirostris*". *Ibis*, 117, 1–6.

366 Marler, P and H Slabbekoorn (2004). *Nature's Music The Science of Birdsong*. Ed. by
367 P Marler and H Slabbekoorn. San Diego: Elsevier.
368 Maynard-Smith, J and D Harper (2003). *Animal Signals*. New York: Oxford University
369 Press.
370 McComb, K and S Semple (2005). "Co-evolution of vocal communication and
371 sociality in primates". *Biology Letters*, 1(4), 381–385.
372 Meise, K et al. (2011). "Sources of acoustic variation: Implications for production
373 specificity and call categorization in chacma baboon (Papio ursinus) grunts".
374 *Journal of the Acoustical Society of America*, 129(3), 1631–1641.
375 Messeri, P et al. (1987). "A study of the vocal repetoire of the banded mongoose
376 (*Mungos mungo*)". *Italian journal of Zoology*, 19(22), 341–73.
377 Nettle, D (2012). "Social scale and structural complexity in human languages".
378 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1597), 1829–
379 1836.
380 Owren, MJ, RM Seyfarth, and DL Cheney (1997). "The acoustic features of vowel-
381 like grunt calls in chacma baboons (*Papio cyncephalus ursinus*): Implications for
382 production processes and functions". *Journal of the Acoustical Society of America*,
383 101(1), 2951–2963.
384 Payne, RS and S McVay (1971). "Songs of humpback whales". *Science*, 173(3991),
385 57–64.
386 Pollar (2011). "Making the most of alarm signals: the adaptive value of individual
387 discrimination in an alarm context". *Behavioral Ecology*, 22(1), 93–100.
388 Randall, JA (1994). "Discriminant of footdrumming signatures by kangaroo rats,
389 *Dipodomys spectabilis*". *Animal Behaviour*, 47(1), 45–54.
390 Rasa, OAE (1986). "Coordinated Vigilance in Dwarf Mongoose Family Groups:
391 The 'Watchman's Song' Hypothesis and the Costs of Guarding". *Ethology*, 71(4),
392 340–344.
393 Schibler, F and MB Manser (2007). "The irrelevance of individual discrimination in
394 meerkat alarm calls". *Animal Behaviour*, 74, 1259–1268.
395 Schütz, AJ (1981). "A Reanalysis of the Hawaiian Vowel System". *Oceanic Linguistics*,
396 20(1), pages.
397 Seyfarth R. M.and Cheney, DL (1984). "The acoustic features of vervet monkey
398 grunts". *The Journal of the Acoustical Society of America*, 75(5), 1623.
399 Seyfarth, RA et al. (2010). "The central importance of information in studies of
400 animal communication". *Animal Behaviour*, 80(1), 3–8.
401 Shapiro, AD (2010). "Recognition of individuals withing social group: signature
402 vocalizations". In: *Handbook of mammalian vocalization*. Ed. by SM Brudzynski.
403 Oxford: Elsevier Academic Press, pp. 495–503.

Slocombe, KE and K Zuberbühler (2007). "Chimpanzees modify recruitment screams as a function of audience composition". *Proceedings of the National Academy of Sciences of the United States of America*, 104(43), 17228–17233.

Snowdon, CT, AM Elowson, and RS Roush (1997). "Social Influences on Vocal Development". In: ed. by CT Snowdon and M Hausberger. Cambride University Press. Chap. Social influences on vocal development in new world primates, pp. 234–248.

Templeton, CN, E Greene, and K Davis (2005). "Allometry of alarm calls: black-capped chickadees encode information about predator size". *Science*, (5730), 1934–1937.

Townsend, SW, C Allen, and MB Manser (2012). "A simple test of vocal individual recognition in wild meerkats". *Biology Letters*, 8(2), 179–182.

Townsend, SW, M Zoettl, and MB Manser (2011). "All clear? Meerkats attend to contextual information in close calls to coordinate vigilance". *Behavioral Ecology and Sociobiology*, 65(10), 1927–1934.

Zuberbühler, K (2002). "A syntactic rule in forest monkey communication". *Animal Behaviour*, 63(2), 293–299.

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CV

Curriculum Vitae

PERSONALIEN

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Species list

Kingdom			
	Class		
	Family		
		Species	Latin name
Plants (**Plantae**)			
	Malpighiales		
	Spurge (Euphorbiaceae)	Euphorbia trees	*Euphorbia candelabrum*
	Salvadoraceae	Bee Sting bush	*Azima tetracantha*
	Caper (Capparaceae)	Woolly Caper bush	*Capparis tomentosa*
	Grasses (Poaceae)		
		Giant rat's tail grass	*Sporobolus pyramidalis*
		Rhodes grass	*Chloris gayana*
	Legumes (Fabaceae)	Acacia spp.	
Animals (Animalia)			
	Birds (Aves)		
	American sparrows (Emberizidae)		
		White-crowned sparrow	*Zonotrichia leucophrys pugetensis*
	Eagles (Accipitridae)		
		African Fish eagle	*Haliaeetus vocifer*
		Martial eagle	*Polemaetus bellicosus*

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Table 1 – *Continued from previous page*

Kingdom	*Class*		
	Family		
		Species	Latin name
	Hamerkop (Scopidae)	Hamerkop	*Scopus umbretta*
	Penguins (Spheniscidae)	Emperor penguin	*Aptenodytes forsteri*
Pipits (Motacillidae)		Meadow pipit	*Anthus pratensis*
	Plovers (Vanellus)	Crowned lapwing	*Vanellus coronatus*
	Stork (Ciconiidae)	Marabou stork	*Leptoptilus crumeniferus*
	Tits (Paridae)		
		Great tit	*Parus major*
		Carolina chickadee	*Poecile carolinensis*
	Mammals (Mammalia)		
	Bears (Ursidae)	Giant panda	*Ailuropoda melanoleuca*
	Bovids (Bovidae)		
		African buffalo	*Syncerus caffer*
		Bohor reedbuck	*Redunca redunca*

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Table 1 – *Continued from previous page*

Kingdom *Class* Family	Species	Latin name
	Bushbug (imbabala)	*Tragelaphus sylvaticus*
	Ugandan kob	*Kobus kob thomasi*
	Waterbuck	*Kobus ellipsiprymnus*
Canids (Canidae)		
	Black-backed jackal	*Canis mesomelas*
	Domestic dog	*Canis lupus familiaris*
	Timber wolf	*Canis lupus*
Cats (Felidae)		
	Leopard	*Panthera pardus*
	Lion	*Panthera leo*
Common bats (Vespertilionidae)		
	Big brown bats	*Eptesicus fuscus*
	Pallid bats	*Antrozous pallidus*
Deer (Cervidae)		
	Fallow deer	*Dama dama*
	Red deer	*Cervus elaphus*

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Table 1 – *Continued from previous page*

Kingdom *Class* Family	Species	Latin name
Dolphins (Delphinidae)		
	Bottlenose dolphins	*Tursiops truncatus*
	Killer whale	*Orcinus orca*
Eared seals (Otariidae)		
	Northern fur sea	*Callorhinus ursinus*
	Australian sea lion	*Neophoca cinerea*
Elephant (Elephantidae)	Afican elephant	*Loxodonta africana*
Herpestids (Herpestidae)		
	Banded mongoose	*Mungos mungo*
	Dwarf mongoose	*Helogale parvula*
	Egyptian mongoose	*Herpestes ichneumon*
	Meerkat	*Suricata suricatta*
	Slender mongoose	*Galerella sanguinea*
	Yellow mongoose	*Cynictis penicillata*
Hyaenas (Hyaenidae)		
	Spotted hyena	*Crocuta crocuta*

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Table 1 – *Continued from previous page*

Kingdom *Class* Family	Species	Latin name
Hippopotamidae	Hippopotamus	*Hippopotamus amphibius*
Horses (Equidae)	Domestic horse	*Equus caballus*
Hominids (Hominidae)		
	Bonobo	*Pan paniscus*
	Chimpanzee	*Pan troglodytes*
	Human	*Homo sapiens*
Hyrax (Procaviidae)	Rock hyrax	*Procavia capensis*
Old-world monkeys (Cercopithecidae)		
	Barbary macaque	*Macaca sylvanus*
	Black-and-white colobuses spp.	*Colobus spp.*
	Campbell's monkey	*Cercopithecus campbelli*
	Chacma baboon	*Papio ursinus*
	Diana monkey	*Cercopithecus diana*
	Gelada	*Theropithecus gelada*
	Japanese macaque	*Macaca fuscata*
	Putty-Nosed monkey	*Cercopithecus nictitans*

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Table 1 – *Continued from previous page*

Kingdom *Class* Family	Species	Latin name
	Pygmy marmoset	*Cebuella pygmaea*
	Rhesus macaque	*Macaca mulatta*
Old-World Porcupines (Hystricidae)		
	Porcupine	*Hystrix africaeaustralis*
Pangolins (Manidae)		
	Ground pangolin	*Manis temminckii*
Pigs (Suidae)		
	Common warthog	*Phacochoerus africanus*
	Giant Forest hog	*Hylochoerus meinertzhageni*
Rorquals (Balaenopteridae)		
	Humpback whale	*Megaptera novaeangliae*
Viverrids (Viverridae)		
	Rusty-spotted genet	*Genetta maculata*

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Table 1 – *Continued from previous page*

Kingdom	*Class*	Family	Species	Latin name
	Reptiles (Reptilia)			
		Crocodiles (*Crocodylidae*)		
			Nile crocodile	*Crocodylus niloticus*
		Lizards (Varanidae)		
			Nile monitor	*Varanus niloticus*
		Pythons (Pythonidae)		
			African rock python	*Python sebae*
		Vipers (Viperidae)		
			African puff adder	*Bitis arietans*